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A DESCRIPTION OF SIX NEW SPECIES OF THE GENUS *CRYPTOCHAETUM* (DIPTERA-AGROMYZIDAE) FROM EAST AFRICA AND EAST INDIES; TOGETHER WITH A KEY TO THE ADULTS AND LARVAE OF ALL KNOWN SPECIES

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(With 30 Figures in the Text)

INTRODUCTION

THE material here described was mostly obtained as a result of a period of study and travel in East Africa in 1939. Two of the species were reared from Coccidae of the genus *Aspidoproctus* at Amani, Tanganyika Territory, and their life history is the subject of an accompanying paper. I am greatly indebted to Dr F. W. Edwards, F.R.S., for allowing me to describe the remarkable species collected by him on Ruwenzori, Uganda, in 1935. I am also most grateful to Dr R. H. Le Pelley of the Scott Agricultural Laboratories, Nairobi, and Dr E. A. Lewis of the Veterinary Research Laboratory, Kabete, Nairobi, for other valuable new material. In addition, The Imperial Institute of Entomology has kindly allowed me to examine and describe material from Uganda in their possession which had been erroneously identified as *Cryptochaetum iceryae* (Will.). Type specimens of all species will be deposited in the British Museum.

The genus as a whole is a striking example of poecilogony, and in almost every species of which the life history is known the larvae provide more obvious specific characters than do the adults. This is perhaps to be expected in a group in which the larvae are elaborately adapted to an endoparasitic mode of life in a particular species of host; but even so one would imagine there can be few other genera in which the phenomenon has been so highly developed. In view of this differentiation those larval and pupal characters which are of particular systematic value have been included under the description of the species, and a key to all known larvae is appended.

In drawing up the descriptions of the adults it would have been desirable to make use of the genitalia had this been possible. Unfortunately, females seem to preponderate in most samples, and in so few cases is adequate material of males available that the use of the genital structures for systematic work is as yet impracticable. It has therefore been necessary to rely mainly on characters already employed by Bezzi, Rondani, Williston and the other early workers. These characters, which consist chiefly of details of the wing

venation and of the structure of the antenna and the head, are not ones which are normally regarded as of particular value for specific distinction in the Diptera; nevertheless, they seem fairly satisfactory for the species of *Cryptochaetum* so far known. Detailed measurements have not been given since size criteria are so unreliable in parasitic groups such as this where the variation in the size of the host and in the number of parasites per host may be so enormous.

The investigations described in these two papers make it quite clear that tropical Africa is an important focus, perhaps the most important focus, of the genus. Indeed, it would not be at all surprising to find that every species of Monophlebine scale insect in Africa has its peculiar species of *Cryptochaetum*.

Nothing has been said here on the vexed question of the relationships of *Cryptochaetum* because I do not feel that the facts forthcoming from the present investigations give any clearer lead on the subject than those already known. It seems better to wait until more members of the genus have been described before reconsidering the matter. One can, however, say that nothing in the present paper seems to contradict the arguments of those recent workers (Hennig, Seguy) who regard *Cryptochaetum* as closely related to the Drosophilidae.

Description of species

Cryptochaetum idiocerum n.sp.

Female. *Total length*, with abdomen fully extended, 5 mm.

General colour: bluish or greenish black with metallic lustre.

Head. Frontal triangle (Fig. 1) sharply pointed, smooth and shining with the lateral margins noticeably, sometimes strongly, indented. Eyes reddish brown with microscopic pale hairs; ocelli reddish, large and placed close together. Post-vertical bristles undifferentiated, hardly longer than rest of hairs on vertex. Fronto-orbital bristles lacking. Parafrontal plates *without* a band of straight parallel grooves forming a margin to the frontal triangle. Parafrontals and genae etched with microscopic parallel wavy lines giving the rest of the head a satiny appearance in contrast to the shining coarsely punctured texture of the thorax and abdomen. *Antennae* (Figs. 2–4) large; longer than the face, brown; third antennal segment very large, 0·9 mm. long, 0·25 mm. wide, and of characteristic shape, tapering towards apex. Third segment completely covered with a dense pile of long curved hairs which are much longer than the apical tubercle and render it difficult to see except under high power.

Thorax brownish black with a metallic lustre giving blue-green reflexions. Mesonotum closely hairy without differentiated bristles, postero-lateral angles brown. Scutellum large with sharp edge, approximately triangular, apex rounded, margins brown. Apical bristles noticeably differentiated. Sternopleura and pteropleura dark reddish brown with margins slightly paler. Halteres straw colour with blackish knobs. *Legs* dark brown, tarsi pale straw

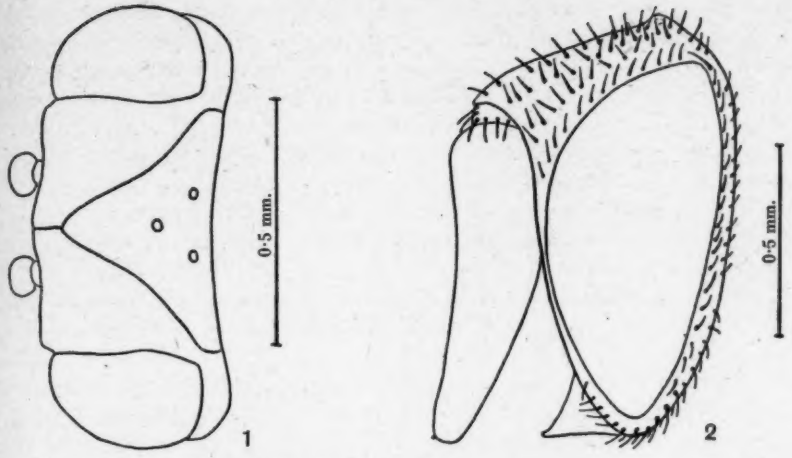

Fig. 1. *Cryptochaetum idiocerum*. Head, dorsal view.
Fig. 2. *Cryptochaetum idiocerum*. Head, lateral view.

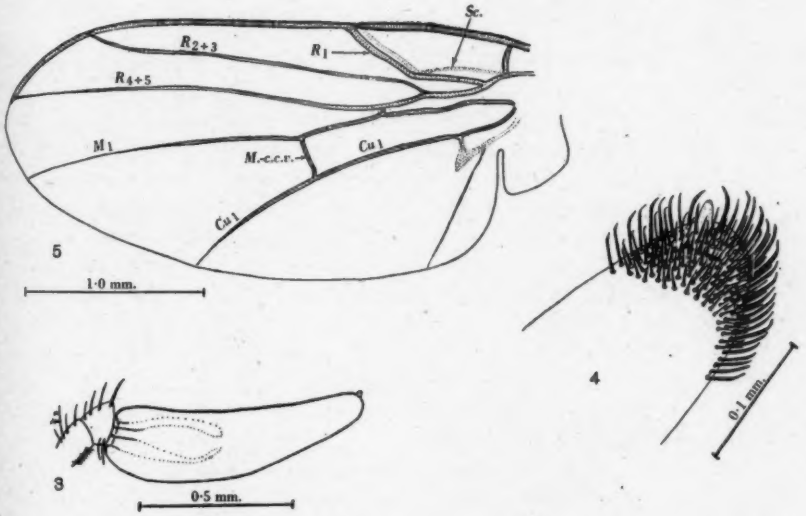

Fig. 3. *Cryptochaetum idiocerum*. Antenna, lateral view.
Fig. 4. *Cryptochaetum idiocerum*. Apex of third antennal segment to show relative size of tubercle and the hairs which cover the whole segment.
Fig. 5. *Cryptochaetum idiocerum*. Wing venation.

colour, tibiae and tarsi beset with short stout dark spines arranged longitudinally in rows, those at apex of each segment slightly longer and stouter than the rest. *Wings* (Fig. 5) large, 3 mm. long, 1·5 mm. broad, hyaline with green and purplish reflexions. Veins pale brown. Costa not extending beyond the end of R_{4+5}, which itself terminates well before the apex of the wing. Subcosta complete and fairly easily distinguishable, markedly angulated. R_{4+5} and M_1 slightly but definitely divergent. R_1 strongly angulated. Radio-medial cross-vein proximal to the junction of R_1 with the costa. Distal portion of Cu_1 much longer than the medio-cubital cross-vein. Medio-cubital cross-vein fairly straight but with a slight kink at its lower end, meeting Cu_1 approximately at right angles.

Abdomen broad at base, tapering sharply to a point; black with metallic green reflexions; clothed with setae and with texture and sculpture very similar to thorax.

Male. Apparently identical save that third antennal segment blunter.

TYPE LOCALITY. Namwamba Valley, 6500 ft. Ruwenzori Range, Uganda. December 1934–January 1935. (F. W. Edwards coll.) Type, paratypes and allotypes with same data all in British Museum.

Host unknown. Larvae and pupae unknown.

The specific name refers to the unusual form of the third antennal segment, by which character this insect is easily distinguishable from all other known species of the genus.

Cryptochaetum striatum n.sp.

Female. *Total length*, with abdomen fully extended, 2·75 mm.

General colour: bluish black with metallic lustre.

Head. Frontal triangle (Fig. 6) small and sharply pointed, smooth and shining, with the lateral margins straight. Eyes deep dull red to bright cherry red in living specimens, according to the amount of illumination, with sparse microscopic hairs; ocelli red, widely spaced. Post-vertical bristles undifferentiated. Fronto-orbital bristles lacking. Parafrontal areas with a broad band of fine straight parallel grooves forming a margin to the frontal triangle. Rest of parafrontals and genae etched with microscopic parallel wavy lines giving the head a satiny texture in contrast to the polished and coarsely punctured surface of thorax and abdomen. *Antennae* (Figs. 7–9) a very little shorter than the face, pale brown. Third antennal segment 0·3 mm. long, 0·13 mm. broad, sharply angled at the apex with a very minute tubercle hardly longer than the antennal hairs.

Thorax bluish black with a metallic lustre, coarsely punctured. Mesonotum closely hairy, without differentiated bristles. Scutellum large approximately triangular with sharp edge, without differentiated bristles. Sternopleura and pteropleura dark reddish brown with paler margins and sutures. Halteres pale brown with black knobs. *Legs* brownish black with pale tarsi. Tibiae not noticeably grooved, spines close packed, not obviously in longitudinal rows.

Tarsi with longitudinal close-packed rows of short stout brown hairs; those at apex of each segment slightly longer and stouter than the rest but truly differentiated bristles absent. *Wings* (Fig. 10) 2 mm. long, 0·9 mm. broad,

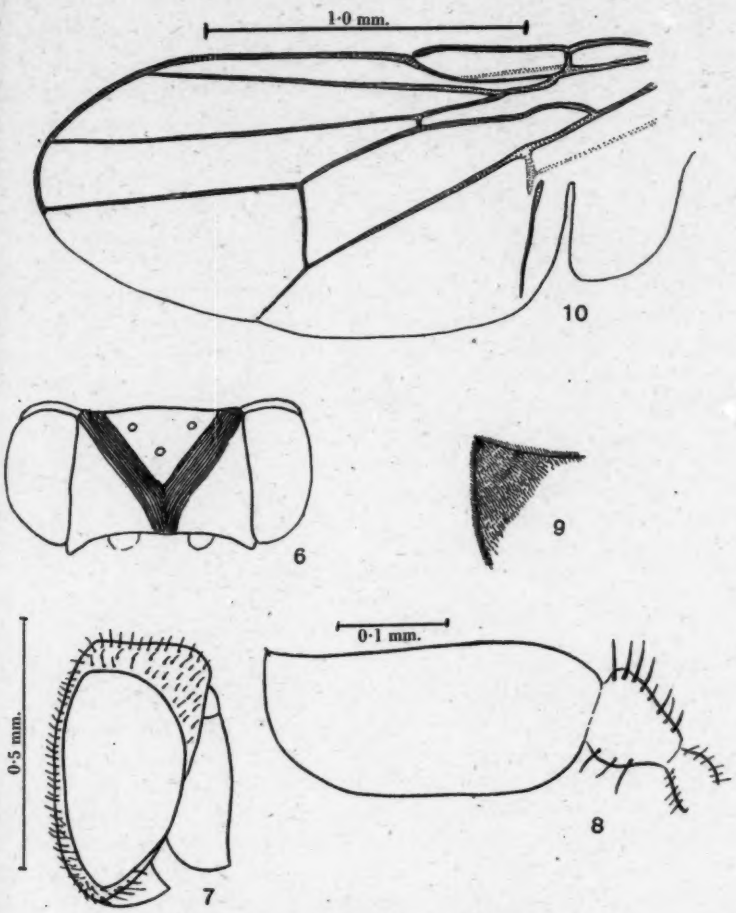

Fig. 6. *Cryptochaetum striatum*. Head, dorsal view.
Fig. 7. *Cryptochaetum striatum*. Head, lateral view.
Fig. 8. *Cryptochaetum striatum*. Antenna, lateral view.
Fig. 9. *Cryptochaetum striatum*. Apex of third antennal segment.
Fig. 10. *Cryptochaetum striatum*. Wing venation.

short and broad, greatest width 1 mm.; hyaline with green and purple reflexions. Veins pale brown. Costa extending to the end of M_1. R_{4+5} terminating just before the apex of the wing, practically parallel with M_1. Radio-medial cross-vein approximately on a level with or slightly proximal

to the junction of R_1 with the costa. Distal portion of Cu_1 about equal to or slightly less than the cross-vein in length. Posterior medio-cubital cross-vein fairly straight but with a slight kink at its lower end, meeting Cu_1 at an angle of about 80°.

Abdomen. Similar to thorax in colour, texture and degree of development of setae.

IMMATURE STAGES. *Second stage larva* (for illustrations see Thorpe, 1941) smooth without body ornamentation of any kind, caudal processes very large, several times length of body.

Third stage larva caudal processes at least five times as long as body, each containing forty or more fine tracheae, anterior spiracles hand-shaped, usually with five fingers, pharyngeal, dentate and median dorsal sclerites well developed, mandibles rudimentary.

Puparium. Posterior spiracles close together, brought far forward, sometimes nearly up to the posterior margin of the operculum.

TYPE LOCALITY. Amani, 3000 ft. East Usambara Mountains, Tanganyika Territory. Holotype. 12 April 1939. Reared from *Aspidoproctus maximus*, of which it is an endoparasite. A large number of the various larval stages and of pupae were obtained but only a single perfect adult was reared. The life history is fully described and the immature stages are figured by Thorpe (1941). Only those characters of the larvae and puparium which provide especially good diagnostic characters are referred to in the above description.

The specific name refers to the striated bands on the parafrontal areas.

Cryptochaetum tuberculatum n.sp.

Total length, 2·5 mm.

General colour: bluish black with metallic lustre.

Head. Frontal triangle large, occupying almost the entire front (Fig. 11); apex blunt, broadly rounded, almost as wide as the distance between the bases of the antennae. Eyes dull reddish brown with microscopic pale hairs; ocelli reddish yellow, small, placed close together. Post-vertical bristles partially differentiated, nearly twice as long as rest of hairs on head. Parafrontal areas uniform dull sooty black in marked contrast to the highly polished frontal triangle. *Antennae* (Figs. 12–14) small, definitely shorter than the face, dark brown, third segment 0·4 mm. long, 0·2 mm. broad, rounded without an apical angle, completely covered with a dense pile of long curved hairs rendering the minute apical spine, which projects only slightly beyond them, difficult to see except under high power.

Thorax black with a metallic lustre, postero-lateral angles of mesonotum and margin of scutellum brown. Mesonotum closely hairy without markedly differentiated bristles. Scutellum large with sharp edge, approximately triangular apex bluntly rounded, apical bristles noticeably differentiated. Sternopleura and pteropleura dark brown with margins slightly paler. Halteres

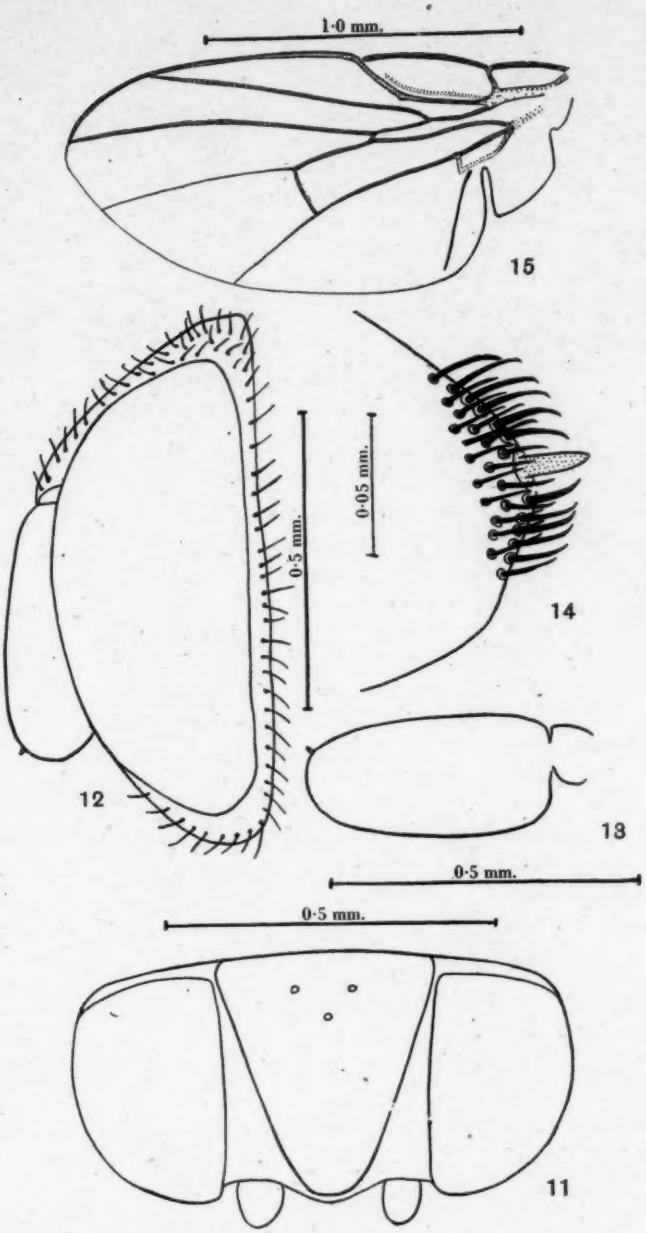

Fig. 11. *Cryptochaetum tuberculatum.* Head, dorsal view.
Fig. 12. *Cryptochaetum tuberculatum.* Head, lateral view.
Fig. 13. *Cryptochaetum tuberculatum.* Antenna, third segment, lateral view.
Fig. 14. *Cryptochaetum tuberculatum.* Apex of third antennal segment to show size of tubercle in relation to the hairs which cover the whole segment.
Fig. 15. *Cryptochaetum tuberculatum.* Wing venation.

pale with black knobs. *Legs* dark brown, tarsi greyish white. Tibiae and tarsi beset with short stout dark spines arranged longitudinally in rows, those at apex of each tarsal segment slightly longer and stouter than the rest. *Wings* (Fig. 15) 1·8 mm. long, 0·8 mm. broad, hyaline with green and purplish reflexions. Veins pale brown. Costa extending to the end of R_{4+5}, which itself terminates slightly before the apex of the wing. Subcosta faintly discernible, not angulated. R_1 definitely angulated. R_{4+5} and M_1 divergent. Radio-medial cross-vein on a level with or slightly proximal to the junction of R_1 with the costa. Distal portion of Cu_1 much longer than medio-cubital cross-vein. Medio-cubital cross-vein almost straight or slightly and evenly curved, not sinuous, meeting Cu_1 approximately at right angles.

Abdomen elongate, tapering, black with metallic green reflexions; clothed with setae and with texture and sculpture very similar to thorax.

Immature stages.[1] *Second stage larva*, caudal processes somewhat shorter than the body, abdominal segments densely clothed with long filaments. Paired pigmented plates on ventral surface of first thoracic segment.

Third stage larva, caudal processes little, if at all, longer than the body, containing few tracheae, quickly degenerating. Anterior spiracles hand-shaped with about 12 "fingers". Mouthparts absent.

Puparium. Short and rounded. Posterior spiracles wide apart.

Type locality. Kwamkoro, Amani, 3000 ft. East Usambara Mountains, Tanganyika Territory. Type and Paratype. 3–12 April 1939. Reared from *Aspidoproctus bifurcatus* Thorpe (1940) and *A. glaber* Lindgr. on *Inga vera* (Leguminosae), in the immature stage of which it is a solitary endoparasite. The life history is described and the immature stages figured by Thorpe (1941), only those characters of the larvae and puparium which provide especially good diagnostic characters are referred to in the above description.

The specific name refers to the long tubercle on the apex of the third antennal segment.

Cryptochaetum brachycerum n.sp.

Total length, with abdomen fully extended, 2·5 mm.

General colour: bluish black with metallic lustre.

Head. Frontal triangle (Fig. 16) broad and blunt, apex as wide as the distance between the bases of the antennae, smooth and shining, margins straight; ocelli reddish yellow, large, well spaced. Post-verticals undifferentiated, hardly longer than rest of hairs on vertex. Fronto-orbital bristles lacking. Parafrontals and genae etched with microscopic parallel wavy lines. Eyes pale reddish brown. *Antennae* (Figs. 17, 18) shorter than the face, pale brown. Front margin of third antennal segment straight, segment itself short and broad, 0·27 mm. long, 0·15 wide, apical angle with a stout conical tubercle, about the same length as the surrounding hairs.

Thorax blackish with a metallic lustre, postero-lateral angles of mesonotum

[1] For illustrations see Thorpe (1941).

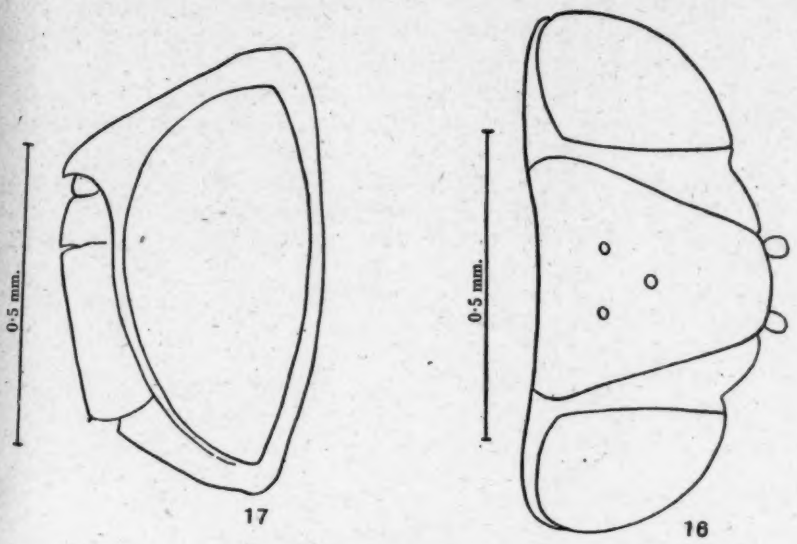

Fig. 16. *Cryptochaetum brachycerum*. Head, dorsal view.
Fig. 17. *Cryptochaetum brachycerum*. Head, lateral view.

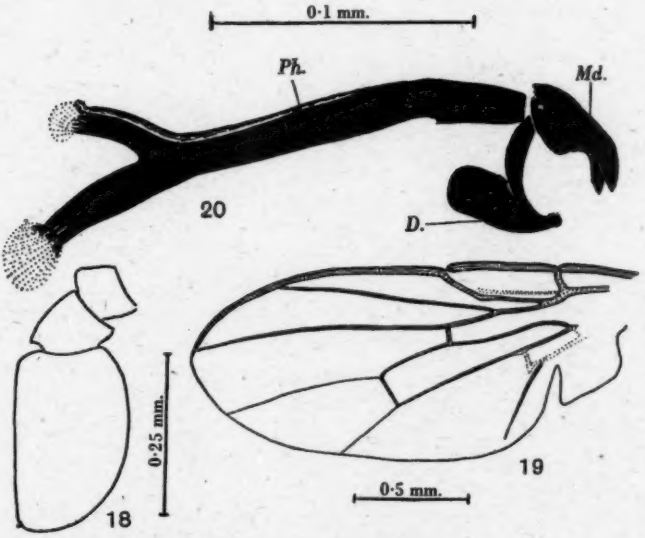

Fig. 18. *Cryptochaetum brachycerum*. Antenna, lateral view.
Fig. 19. *Cryptochaetum brachycerum*. Wing venation.
Fig. 20. *Cryptochaetum brachycerum*. Mouthparts of second instar larva.

and margin of scutellum brown, scutellum large with sharp edge approximately triangular, apex bluntly rounded, apical bristles *not* differentiated. Sternopleura and pteropleura brown. Halteres pale with black knobs. *Legs* dark brown, tarsi whitish. Tibiae and tarsi beset with stout brown spines, those at the apex of the tarsal segments little, if at all, longer or stouter than the rest. *Wings* (Fig. 19) 2 mm. long, 0·8 mm. broad. Costa extending to the end of R_{4+5} which itself terminates slightly before the apex of the wing. Subcosta faintly discernible, incomplete, not markedly angulated. R_1 definitely angulated. R_{4+5} and M_1 *very* slightly divergent. Radio-medial cross-vein slightly

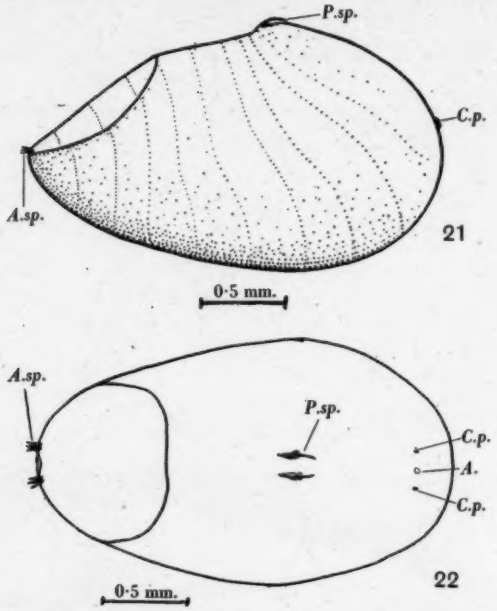

Fig. 21. *Cryptochaetum brachycerum.* Puparium, lateral view.
Fig. 22. *Cryptochaetum brachycerum.* Puparium, dorsal view.

proximal to or almost on a level with the junction of R_1 with the costa. Distal portion of Cu_1 about 1½ times the length of the medio-cubital cross-vein. Medio-cubital cross-vein straight, meeting Cu_1 approximately at right angles.

Abdomen similar to other species described, no special features observed.

Immature stages. *Second stage larva*, only cast skin available, having well-developed mouthparts (Fig. 20), the pharyngeal sclerite being unusually long and slender.

Puparium (Figs. 21, 22) showing anterior hand-like spiracles with five "fingers"; posterior spiracles close together. Pharyngeal sclerite developed but mandibles and dentate apparently lacking.

Type locality. Lambwe Valley, Southern Kavirondo, Kenya. Four

adult specimens (syntypes) bred by Dr E. A. Lewis in December 1937 from "*Monophlebus*" sp.[1] on *Acacia seyal* var. *fistulina*, it being a gregarious endoparasite of the scale insect. Dr Lewis had presented the specimens to the museum of the Entomological Department of the Scott Agricultural Laboratories, Nairobi, and I am indebted to Dr R. H. Le Pelley for kindly allowing me to examine and describe the material. Unfortunately, all the specimens are in such bad condition that it has not been possible to select a single one as the type. I have therefore drawn up the description from all the available specimens which are thus syntypes.

In some respects the species is close to *Cryptochaetum tuberculatum* from which, however, it can be readily distinguished by the shape of the third antennal segment, and the straight and relatively short medio-cubital crossvein. The wing of *C. tuberculatum* is also somewhat broader with the result that R_{4+5} and M_1 are more divergent from one another and the distal portion of Cu_1 is relatively longer. The species is even more readily distinguished in the immature stages by the mouthparts (second stage) and the anterior spiracles (third stage) having only five fingers.

C. brachycerum also appears closely related to *C. curtipenne* (Knab) bred from *Walkeriana kandyense*, Green, in Ceylon. Unfortunately, Knab's description besides lacking all illustrations is so inadequate and the types and paratypes in such poor condition that it is difficult to know what the distinguishing features of *curtipenne* are. However, Knab's description of the wings as "very broad" and of the third antennal segment as having "the apex drawn out into an acute point in front" would certainly not fit *C. brachycerum*.

BIOLOGICAL NOTES. It lives gregariously in its host, at least three specimens being able to reach maturity as parasites of a single individual. Both anterior and posterior spiracles project through the host body wall at the time of pupation and, as one would expect from its gregarious habit, no special attitude is necessary for successful pupation. At least one of the specimens emerged from a male coccid puparium. Dr Lewis is kindly attempting to procure me more material of this interesting species, but until this is forthcoming no further details of the biology can be given.

The specific name of course refers to the very short and broad third antennal segment.

Cryptochaetum oocerum n.sp.

Female. *Total length*, with abdomen fully extended, 2·5 mm.

General colour: bluish or greenish black with metallic lustre.

Head. Frontal triangle (Fig. 23) broad and blunt, apex as wide as the distance between the antennae, smooth and shining, margins straight, ocelli cherry red, small. Post-vertical bristles partially differentiated, nearly twice as long as rest of hairs on head. Fronto-orbital bristles lacking. Parafrontal

[1] This insect, which clearly represents a new species, falls within the genus "*Monophlebus*" in the wide sense, as used by Green, but does not seem to find a place in any of the sub-divisions of the genus given by Morrison (1928). I am sending material to Dr Morrison for examination.

areas and genae dull sooty black. Eyes dull brownish yellow. *Antennae* (Figs. 24–26) shorter than face, pale brown; third antennal segment 0·3 mm. long, 0·15 mm. broad, approximately oval, apical angle with a stout conical tubercle (Fig. 26) about the same length as the surrounding hairs.

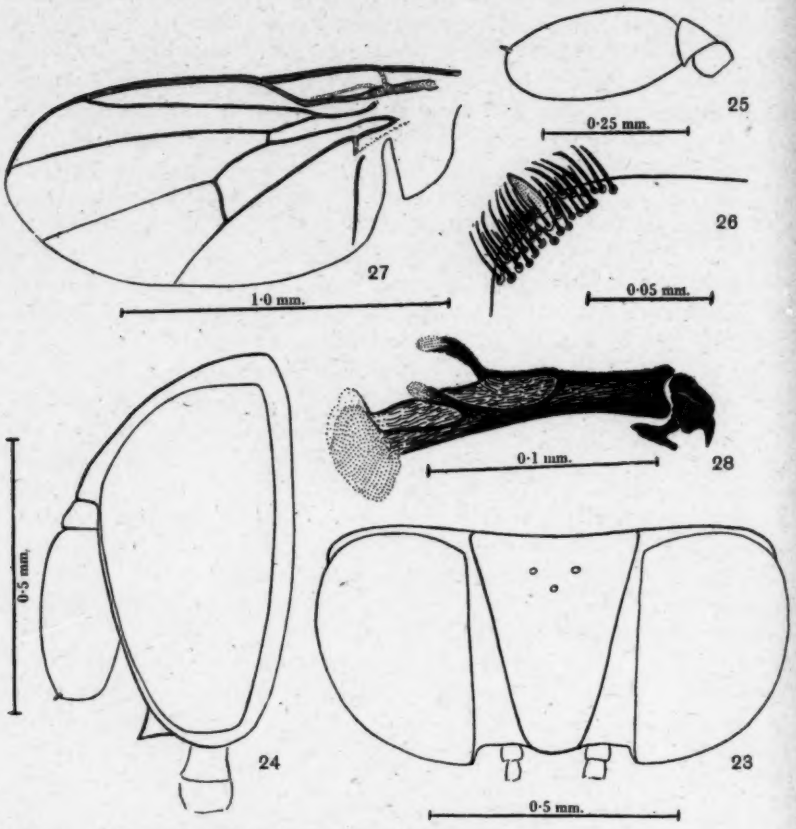

Fig. 23. *Cryptochaetum oocerum*. Head, dorsal view.
Fig. 24. *Cryptochaetum oocerum*. Head, lateral view.
Fig. 25. *Cryptochaetum oocerum*. Antenna, lateral view.
Fig. 26. *Cryptochaetum oocerum*. Apex of third antennal segment.
Fig. 27. *Cryptochaetum oocerum*. Wing venation.
Fig. 28. *Cryptochaetum oocerum*. Mouthparts of second instar larva.

Thorax bluish black with a metallic lustre, mesonotum and scutellum uniform bluish black, scutellum large with sharp edge, approximately triangular, apex bluntly rounded, apical bristles differentiated, six of them being twice as long and stout as the remainder of the setae on the scutellum. Sternopleura and pteropleura brown. Halteres pale with black knobs. *Legs*

brown, tarsi whitish. Tibiae and tarsi beset with stout dark spines arranged longitudinally in rows, those at apex of each segment definitely longer and stouter than the rest. *Wings* (Fig. 27) 1·5 mm. long, 0·65 mm. broad, costa extending to the end of R_{4+5} which itself terminates slightly before the apex of the wing. Subcosta faintly discernible, curved, incomplete, merging with R_1 at or slightly before the angle of the latter. R_1 definitely angulated. R_{4+5} and M_1 slightly divergent. Radio-medial cross-vein slightly distal to the junction of R_1 with the costa. Distal portion of Cu_1 about twice the length of the medio-cubital cross-vein. Medio-cubital cross-vein slightly sinuous meeting Cu_1 at an angle of approximately 75°.

Abdomen similar to other species described; no special features observed.

IMMATURE STAGES. *Second stage larva* (Fig. 28), shows the mouthparts from a cast skin.

Puparium showing anterior hand-like spiracles with usually seven "fingers", two of which are very long, one of intermediate length and the others very short. Pharyngeal sclerite developed but mandibles apparently lacking. Posterior spiracles fairly close together, long and very slender. Pharyngeal sclerite normally developed, dentate apparently represented but no mandibles found.

TYPE LOCALITY AND HOST. Praja. Lombok, North-east Indies. Two female specimens (syntypes) bred by Mr R. H. Le Pelley, 22 May 1937. They were parasitizing a scale insect of uncertain identity living upon *Achras zapota* (Sapotaceae), and which, until further evidence is forthcoming, I assume to be a Monophlebine scale. Actually Mr Le Pelley, without microscopic examination, tentatively identified the host as a *Pseudococcus*. If this were correct it would provide the first exception to the rule that *Cryptochaetum* is exclusively a parasite of scale insects of the subfamily Monophlebini. The puparia of the parasite still retain the skins of their hosts although in a very fragmentary condition. I have examined these carefully and in one case have found abdominal spiracles. In the other specimens the anal structure can also be seen fairly well, and this as far as I can ascertain does not agree with *Pseudococcus*, but is appropriate, as is the presence of abdominal spiracles, to the family Margarodidae which contains the Monophlebini.

It is worthy of note, however, that according to Morrison (1928) the Pseudococcinae are obviously the closest relatives of the Margarodidae.

Both specimens of the parasite are in perfect condition but are preserved in alcohol, so that notes on the coloration are of doubtful value. I am much indebted to Mr Le Pelley for allowing me to examine and describe the material.

This species seems very close to the Australian *C. monophlebi* of Skuse, from which, however, it can be readily distinguished by the distinct angle of R_1 and the incomplete subcosta. Moreover, according to the original description *monophlebi* is a smaller insect and has deep blue instead of brown legs. The antennae of *monophlebi* are not figured, but Skuse's description gives no definite basis for separation on this character.

Biological notes. Little biological information can be gleaned from the material in my possession. It is of course an endoparasite and only one puparium is formed per host. The puparium is formed upside down in the scale insect, the head region of the parasite being directed posteriorly. Both anterior and posterior spiracles project through the host's body wall, the latter piercing the body wall in between the metathoracic legs. The specific name refers to the oval third antennal segment.

Cryptochaetum pariceryae n.sp.

Total length, with abdomen fully extended, 2·5 mm.

General colour: bluish black with metallic lustre.

Head. Frontal triangle large, occupying almost the entire front; apex blunt, broadly rounded, almost as wide as the distance between the bases of the antennae. Eyes dull reddish brown with microscopic pale hairs; ocelli small, reddish, placed close together. Post vertical bristles relatively well differentiated, in some specimens nearly twice as long as rest of hairs on head.

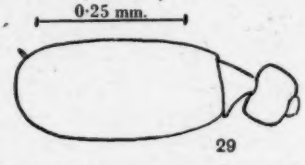

Fig. 29. *Cryptochaetum pariceryae.* Antenna, lateral view.

Parafrontal areas uniform dull sooty brown in marked contrast to the highly polished frontal triangle. *Antennae* (Fig. 29) small, slightly shorter than face, third segment rounded, 0·35 mm. long, 0·16 mm. broad, without an apical angle, completely covered with a dense pile of long hairs, rendering the apical spine, which does not project beyond them, difficult to see except under high power.

Thorax bluish black with a metallic lustre, margin of scutellum and postero-lateral angles of mesonotum brown. Mesonotum closely hairy without markedly differentiated bristles. Scutellum large with sharp edge, approximately triangular with apex bluntly rounded, apical bristles noticeably differentiated. Sternopleura and pteropleura brown. Halteres pale brown with blackish lobes. *Legs* dark brown, tarsi pale straw colour. Tibiae and tarsi beset with short stout dark spines arranged longitudinally in rows, those at apex of each tarsal segment slightly stouter than the rest. *Wings* (Fig. 30) 1·76 mm. long, 0·77 mm. broad, hyaline with green and purple reflexions. Veins pale brown. Costa extending to the end of R_{4+5} or a very little beyond, thus terminating practically at the apex of the wing; subcosta discernible, complete, not angulated. R_1 definitely angulated. R_{4+5} and M_1 slightly divergent. Radio-medial cross-vein very slightly if at all proximal to the

junction of R_1 with the costa. Distal portion of Cu_1 nearly twice the length of the medio-cubital cross-vein. Medio-cubital cross-vein straight except for a slight curve at its posterior end, as a whole running at an angle of about 75° or 80° to proximal part of Cu_1, but owing to its bend actually meeting it at right angles.

Abdomen elongate, tapering, black with metallic green reflexions; clothed with setae and with texture and sculpture very similar to thorax.

IMMATURE STAGES. An endoparasite on immature stages of its host. Larvae unknown except for certain features of the third stage which can be seen in the puparium. They are as follows: Anterior spiracles hand-like with six "fingers", two very long. Posterior spiracles normal. Mouthparts apparently complete, including both mandibles and dentate. Puparium solitary, inverted, with both pairs of spiracles projecting through the body wall.

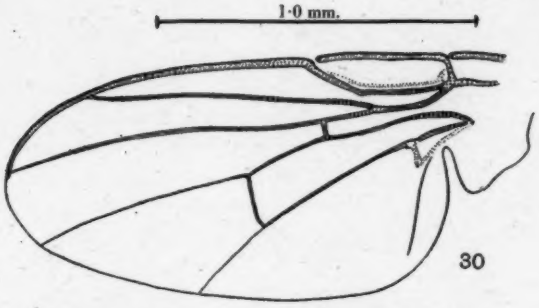

Fig. 30. *Cryptochaetum pariceryae*. Wing venation.

TYPE LOCALITY. Kampala, Uganda. Ten adult specimens; type, paratypes and allotypes reared from a species of *Icerya* by Mr Hargreaves in November 1930 and presented by him to the Imperial Institute of Entomology. Now in the collections of the British Museum. These specimens were submitted to Dr Hendel who wrongly identified them as *Cryptochaetum iceryae* (Williston). They are the specimens mentioned by him in his 1933 paper (see p. 99), and they are certainly closer to *iceryae* than to any other known species of *Cryptochaetum*. Nevertheless, several characters seem to offer reliable means of distinguishing the two. These are: (1) The relatively high degree of differentiation of the post-vertical bristles. (2) Radio-medial cross-vein very slightly if at all proximal to the junction of R_1 with the costa. (3) Medio-cubital cross-vein straight except for a very slight curve at its posterior end. (4) Distal portion of Cu_1 less than twice the length of the medio-cubital cross-vein. (5) Anterior spiracles of third stage larva hand-like with six fingers. Of these five characters the last is by far the most readily observed if material of larva or puparium is available, and it is probably also the most reliable.

The specific name refers to the close resemblances of the adult to the Australian species *C. iceryae*.

Key to the known species of the genus Cryptochaetum *adults*

1. Frontal triangle small, sharply pointed, the point much narrower than the distance between the bases of the antennae 2

   Frontal triangle large, occupying almost the entire front, the apex blunt and almost as wide as the distance between the bases of the antennae 6

2. (1) Wings with costa extending to the end of M_1 3

   Wings with costa extending only to the end of R_{4+5} or a little beyond . . 4

3. (2) Wings slightly infuscated, R_{4+5} terminating at the apex of the wing, slightly divergent from M_1. Antennae a little longer than the face. Parafrontal areas not striate **fastidiosum** Bezzi

   Wings hyaline, R_{4+5} terminating a little before the apex of the wing, practically parallel with M_1. Antennae not longer than the face. Parafrontal areas striate **striatum** Thorpe

4. (2) R_{4+5} terminating at the apex of the wing, last section of the cubitus less than twice the length of the medio-cubital cross-vein, wings and body 3 mm. long **aenescens** De Meijère

   R_{4+5} terminating before the apex of the wing, distal portion of the cubitus more than twice the length of the medio-cubital cross-vein 5

5. (4) Antennae elongated and tapering of distinctive shape, total length of insect 5 mm., wings 3 mm. Margins of frontal triangle slightly sinuate **idiocerum** Thorpe

   Antennae large but rounded. Insect smaller, wings 2 mm. or a little over **grandicorne** Rondani

6. (1) Fore-tarsi of male strongly dilated **latimana** Malloch

   Fore-tarsi of male normal 7

7. (6) Radio-medial cross-vein definitely proximal to the junction of R_1 with the costa 8

   Radio-medial cross-vein very slightly if at all proximal to the junction of R_1 with the costa, sometimes definitely distal 10

8. (7) Medio-cubital cross-vein straight and complete 9

   Medio-cubital cross-vein curved or sometimes incomplete, distal portion of Cu_1 more than twice the length of the medio-cubital cross-vein **iceryae** (Will.)

9. (8) Third antennal segment rounded at apex, distal section of M_1 normal **chalybeum** De Meijère

   Third antennal segment prolonged at the upper angle to a sharp point, distal section of M_1 faint and indistinct **curtipenne** Knab

10. (7) R_1 evenly and smoothly curved **monophlebi** (Skuse)

    R_1 with a distinct angle 11

11. (10) Antenna definitely longer than the face **buccatum** Hendel

    Antenna not longer than the face 12

12. (11) Antenna little if at all shorter than the face **pariceryae** Thorpe

    Antenna shorter than the face 13

13. (12) Third antennal segment "with apex drawn out into an acute point in front" **curtipenne** Knab

Third antennal segment not so produced 14

14. (13) Upper (anterior) margin of third antennal segment straight, segment short and stout of characteristic shape **brachycerum** Thorpe

Upper (anterior) margin of third antennal segment evenly curved . . . 15

15. (14) Subcosta incomplete, coalescing with R_1 just before the angle; radio-medial cross-vein slightly distal to the junction of R_1 with the costa. Medio-cubital cross-vein slightly sinuous **oocerum** Thorpe

Subcosta faint but complete or nearly so, at least distinguishable well beyond the angle; radio-medial cross-vein on a level with or very slightly proximal to the junction of R_1 with the costa. Medio-cubital cross-vein evenly curved **tuberculatum** Thorpe

Key to the known third stage larvae of the genus Cryptochaetum

1. Mouth apparatus complete; having pharyngeal, mandibular and dentate sclerites 2

Mouth apparatus either degenerate or entirely absent 5

2. (1) Anterior spiracles dart-like **iceryae**

Anterior spiracles shaped like a hand with a number of separate fingers . . 3

3. (2) Anterior spiracles with five or more fingers 4

Anterior spiracles with four fingers, caudal processes very short, less than one-quarter of body length **buccatum**

4. (3) Anterior spiracles with five fingers, the shortest about half the length of the longest **grandicorne**

Anterior spiracles with six fingers, the shortest less than one-third the length of the longest, which are very long and slender **pariceryae**

5. (1) Mandibles lacking but pharyngeal and dentate sclerites normal . . . 6

Both mandibles and dentate absent and pharyngeal sclerite if present unpigmented 7

6. (5) Anterior spiracles with seven fingers **oocerum**

Anterior spiracles with five fingers, caudal processes five times the length of body, or more **striatum**

7. (5) Anterior spiracles with 12 or more fingers, caudal processes little longer than the body **tuberculatum**

Anterior spiracles with seven fingers, caudal processes several times as long as body **chalybeum**

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Lettering of Figures

A. anus; *A.sp.* anterior spiracle; *C.p.* point of attachment of caudal processes; *Cu.* first cubital vein; *D.* dentate sclerite; *M.* first median vein; *M.-c.c.v.* medio-cubital cross-vein; *Md.* mandibular sclerite; *P.sp.* posterior spiracle; *Ph.* pharyngeal sclerite; *R.* radius; *Sc.* subcosta.

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THE BIOLOGY OF *CRYPTOCHAETUM* (DIPTERA) AND *EUPELMUS* (HYMENOPTERA) PARASITES OF *ASPIDOPROCTUS* (COCCIDAE) IN EAST AFRICA

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(With 26 Figures in the Text)

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1. Introduction

Tropical and certain parts of subtropical Africa constitute the home of the genus *Aspidoproctus* (Coccidae, Monophlebini). The genus is remarkable in several ways, but chiefly because of the very large size attained by some of the species. *A. maximus* and *A. giganteus* are almost certainly the largest scale insects in the world, the female being well over 1 in. long and as much as $\frac{3}{4}$ in. thick. Owing to the relatively degenerate structure of scale insects in general, and in particular because of the poor development of the circulatory and tracheal systems, the biology of scale-inhabiting parasites is always of interest. This is particularly the case in relation to problems of respiration, and many scale parasites are already known (Thorpe, 1931, 1934, 1936) which exhibit very striking respiratory adaptations. Previous to the present paper no parasites had been recorded from the genus *Aspidoproctus*, yet it appeared extremely improbable on general grounds that these insects were immune from the attacks of the usual dipterous and hymenopterous parasitoids. Accordingly, when opportunity came to visit East Africa, attention was directed particularly to this problem; for it was felt that with insects of such large size and having such a thick dorsal cuticle, the problems to be overcome

by the internal parasite would be intensified tenfold, and that any species found would be likely to exhibit structural and physiological adaptations of unusual interest. That this is indeed the case the present paper will show.

Before proceeding further I would like to express my very great indebtedness to the Director and Staff of the East African Agricultural Research Station at Amani, Tanganyika Territory, for the most generous help and kindness shown during my visit there. Similarly in Southern Rhodesia the ready assistance so kindly given by Dr W. J. Hall of the Mazoe Experiment Station of the British South Africa Co., and by Messrs R. W. Jack and A. Cuthbertson of the Entomological Laboratory of the Department of Agriculture at Salisbury was of great value in securing much interesting material. I would also like to express my gratitude to the Leverhulme Trustees, who by the award of a Research Fellowship made the investigation possible. To my wife I am indebted for much assistance in both field and laboratory at Amani.

2. Structure and biology of *Aspidoproctus maximus*

The strikingly large size of many species of the genus *Aspidoproctus* has already been mentioned, but this is by no means the only point of interest in the genus, and a brief outline of the structure and biology must be given. Morrison (1928) lists eighteen species of this genus known from Africa, and two more have since been described (Thorpe, 1940). No doubt many others await description. As far as is known they are almost entirely confined to trees of the family Leguminosae. The most remarkable structural peculiarity of *Aspidoproctus* (shared also by the allied genera *Perissopneumon*, *Labioproctus* and *Pseudaspidoproctus*) is the existence in the female of a large marsupium or brood pouch (see Fig. 1) which consists of a deep invagination of the ventral wall of certain abdominal segments. Into the pouch formed by this invagination opens the oviduct. The external opening of the pouch is greatly narrowed and is almost completely covered by a stout triangular flap of felted waxen threads secreted by specialized gland cells on the margin of the opening. The eggs as they ripen are passed into this pouch and remain there until hatching, and during the latter part of the life of the female the pouch becomes completely filled with a mass of eggs and newly hatched young. Soon after the young are hatched they make their way out, crawling on to the branches and foliage of the tree to which the parent is attached.

As will be seen from Fig. 1 the dorsal body wall of the scale insect is thick and hard. It is very well supplied with wax glands and the insect in consequence is thickly covered with a waxen powder, and there are also hard stout brushes of yellowish white wax projecting at intervals round the margin. Although the insects are very large, this waxy covering and ornamentation renders them extremely difficult to see on the boles of the trees on which they live. At a little distance they appear very like oval patches of lichen. Males have been recorded but they appear to be extremely rare.

The species with which we are particularly concerned in this study is *Aspidoproctus maximus* Newstead (1910) [=*Lophococcus maximus*, Sanders MSS.]. This species is known from Tanganyika and Kenya in the north to Southern Rhodesia in the south. It may occur in parts of Uganda, but appears to be replaced by other species in West Africa. I have observed it attacking the following leguminous plants: *Cassia siamea*, *Adenothera racemosa*, *Albizzia stipulata*, *Schizolobium excelsa* and *Brachystegia randii*. Lindinger (1913) in Tanganyika has also recorded it from the teak, *Tectona grandis*, and Brain (1915) recorded it from *Grevillea robusta* in Southern Rhodesia. While it does not appear to be of any particular economic importance in East Africa, it has given rise to considerable trouble in Southern Rhodesia, and Lounsbury (1908) has placed on record a very troublesome infestation on shade trees (*Brachystegia*, *Grevillea*) in the neighbourhood of Salisbury in 1908. Describing the infestation in one particular area he says: "Hereabouts the insect thickly studs the trunks and larger branches often in an unbroken layer yards in length on the limbs, and the general appearance of the trunks and of the ground beneath many of the trees is as if thin treacle had been sprayed over the surface." Lounsbury also mentions instances of this scale being found occasionally on *Casuarina* and *Hibiscus* and also "grape, citrus, eucalyptus and a flamboyant tree", but it does not appear certain that it can reach maturity on any of these hosts.

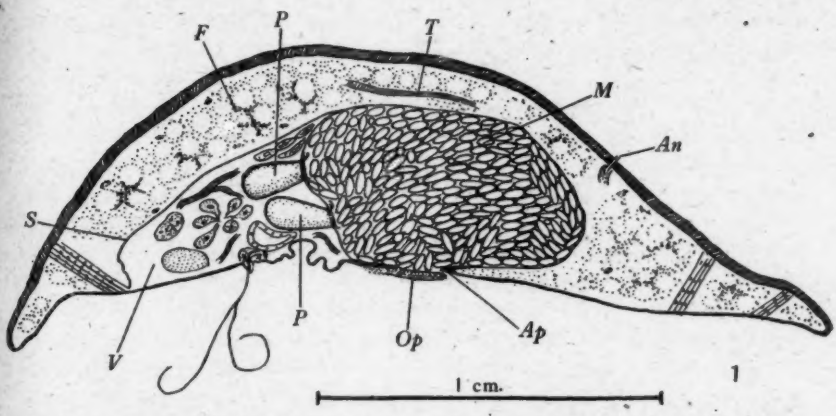


Fig. 1. Diagrammatic sagittal section of *Aspidoproctus maximus* to show main features of anatomy and also position assumed by *Cryptochaetum striatum* for pupation.

The fact that no further instances of outbreaks of economic proportions have been recorded from Rhodesia suggests that *Aspidoproctus maximus* may be normally kept in check by parasites, and that it is only on very rare occasions that it escapes from this break on its multiplication. I found abundant evidence of the activity of *Cryptochaetum* at Salisbury, but it appears to be

another new species which is concerned and I was unfortunately unable to rear it.

The young *Aspidoproctus maximus* are very active when they first emerge from the parent's pouch. In the first instar there is no trace of the stout waxy horns or brushes mentioned above, but almost immediately after hatching a number of very long hair-like waxy filaments are secreted by large bilocular tubular pores situated all round the margin of the body.[1] The filaments are at first backwardly directed so that they trail out behind the crawling insects, being at least three or four times the length of the body itself. As soon as the young insect escapes to the outside from the pouch of its parent, the filaments come to project at right angles to the body and the effect of this is to give a very large wind resistance to the young insect. It is almost as easily blown about as a thistledown, and I have little doubt that this is the usual method of transference although birds and flying insects may play some part as carriers. I know of no comparable instance of adaptation for wind dispersal among immature insects.

Having been blown or carried to another branch or another tree of a suitable species, or perhaps after having merely crawled to another part of the tree, the young insect commences feeding on leaves or shoots. After a short while it moults to the second instar, which lacks the long lateral filaments, but shows the first trace of the stout marginal brushes. During the first two or three instars the animal is remarkably active for a scale insect, and readily moves from place to place on the tree. As it gets larger it descends to feed on the thicker branches or on the trunk, it being now able to pierce very thick bark indeed. Another peculiarity of structure of this genus is the dorsal position of the anus (Fig. 1). The anal orifice is very minute and is surrounded by a group of wax glands which secrete a waxen tube, perhaps half a millimetre in diameter, which projects at right angles from the back of the animal. It may attain a length of 2 or 3 mm. before it is broken off. Through this tube is passed the honey-dew, which at times is produced in great quantity. According to Lounsbury it can be forcibly ejected to a considerable distance, but I myself have not observed this. The young scale insects are remarkably attractive to ants; indeed the attendant ants afford the easiest way of finding them on the tree trunk. The ants stand beside them, continually stroking them and drinking the honey-dew as it is produced. They are so persistent in their attentions that they often brush away all the waxy powder which normally covers the scale and they not infrequently bite off the waxen tube. Lounsbury also says: "Ants gather to get the liquid and a certain small bird which frequents the Kopje is evidently very fond of it, poking the insect with its beak to get it." I have not, however, observed birds displaying any interest in the scale in Tanganyika.

[1] These waxy filaments are extremely delicate and are almost invariably destroyed by preservatives and fixatives. One can however assume them to be present in the first instars of the allied genera *Pseudaspidoproctus, Monophleboides, Nietnera, Walkeriana, Hemaspidoproctus* and *Labioproctus*, all of which show the characteristic pores (Morrison, 1928).

As development continues, the scale insect becomes increasingly sluggish and finally loses all power of movement. In the latter stages the dorsal body wall becomes exceedingly thick and hard, and this in itself constitutes a big problem for any insect parasite.

The great marsupium or brood pouch and other striking structural characteristics of *Aspidoproctus* have been referred to above, and it is not necessary here to describe the internal anatomy of the scale in great detail. From the point of view of the life history of the parasites, however, it is important to draw attention to the well-developed supravisceral membrane separating the visceral region from the great part of the body cavity lying above it which contains an immense quantity of fat body. The Malphigian tubes are also interesting. They are three in number; two of these are simple and the remaining one divides into six branches, thus giving the appearance of eight in all. The gut is elaborately looped and coiled, and it appears doubtful whether there is a complete passage through, although it is difficult to be quite sure of this point and further investigations are in progress. Most probably, as in certain other Hemiptera, the honey-dew passes into the rectum by diffusion.[1] Thoracic and abdominal spiracles are present, and although the tracheal system does not compare in degree of development with active insects of similar size, it is by no means poorly developed. At first sight it might appear that a fully grown *A. maximus* must be near the limit of size at which a tracheal system, acting by diffusion alone, can be adequate. If the insect were a solid mass of tissue then indeed it would seem that mechanical ventilation would be essential. But the fact that so much of the total volume of the insect is taken up by the thin-walled marsupium, which of course contains air and is open to the exterior, alters the situation; this must lighten considerably the strain on the tracheal system.

From this preliminary survey it will be seen that besides overcoming difficulties of respiration, any insect parasites must also have special adaptations in order to enable them to invade the host through the thick body wall, and also to enable them to emerge when their development is complete.

3. THE BIOLOGY OF PARASITES OF *ASPIDOPROCTUS MAXIMUS* AND *BIFURCATUS*

(i) *Diptera*

In two previous papers (1931, 1934) the writer has been concerned with the biology and development of two species of an aberrant dipterous genus *Cryptochaetum*, parasitic on monophlebine scale insects in different parts of the world. This genus, *Cryptochaetum*, is remarkable from many points of view. Adult characteristics will not here be dealt with, since they are discussed in the accompanying systematic paper (Thorpe, 1941); suffice it to say that the genus

[1] This and many other problems of physiological and morphological interest require further investigation. It was hoped to continue these studies in England but unfortunately the recent suspension of the air mail has made this impossible for the present.

has been placed in at least four families of the Acalypterates: Octhiphilinae, Milichiidae, Agromyzidae, Drosophilidae. *Cryptochaetum* has not hitherto been known to occur in Africa south of the Sahara except for a mistaken record of *C. iceryae* from Uganda, and some specimens collected by F. W. Edwards in Ruwenzori and described in the accompanying paper. The first known species was described from the Mediterranean area, being found in southern Europe. Several species occur in Australia, one of which has been successfully introduced into North America. Others are known from the Orient and the East Indies. Since *Aspidoproctus* belongs to the same subfamily attacked by this genus in other parts of the world, it was anticipated that investigation in Africa would reveal the presence of *Cryptochaetum* over a wide area, and this expectation was fulfilled. In the accompanying paper (Thorpe, 1941) six new species are described, five of them from Africa and one from the north-east Indies. The biology of only two of these has as yet been followed. They are both parasites of *Aspidoproctus* and are dealt with below.

(*a*) Cryptochaetum striatum *Thorpe*.

The host of this parasite is *Aspidoproctus maximus*, the biology of which has already been summarized in the preceding section. As with many other members of the genus *Cryptochaetum*, the eggs are apparently placed in the body cavity of the half-grown scale, a puncture being made through the body wall before this has acquired the hard tough texture of the fully grown insect. The duration of the egg stage has not been worked out, but first-stage larvae on the point of moulting have been discovered in the body cavity of mature females. This suggests that the egg stage may be of some considerable duration. The first stage larva itself appears to be very similar in essentials to that of *Cryptochaetum iceryae* (Thorpe, 1931): mouthparts, spiracles and segmentation are lacking entirely; the tracheal system is not yet developed, and there are the same caudal processes containing blood. These, however, as will be seen from the illustration (Fig. 2), are very much longer than in the first stage of *iceryae*. They may attain a length of three times that of the body. There is no indication of an open mouth and there was no sign of food in the gut. Any nutriment that is taken must be absorbed by diffusion through the cuticle.

The second-stage larva (Fig. 3) shows the usual segmentation, and has normally developed mouthparts. The tracheal system is now well developed, though there are no spiracles. There are tracheal branches penetrating the caudal filaments for a considerable distance. They are similar to those of the third stage, though not so numerous. As will be seen from the illustration (Fig. 3) the caudal filaments have increased considerably in size. These second-stage larvae lie loose in the blood, often in the peripheral region of the scale. From an examination of the gut content, it appears that they feed largely on the blood, taking only a small proportion of the bright yellow fat body of the host. This stage differs from all known second-stage larvae of this genus

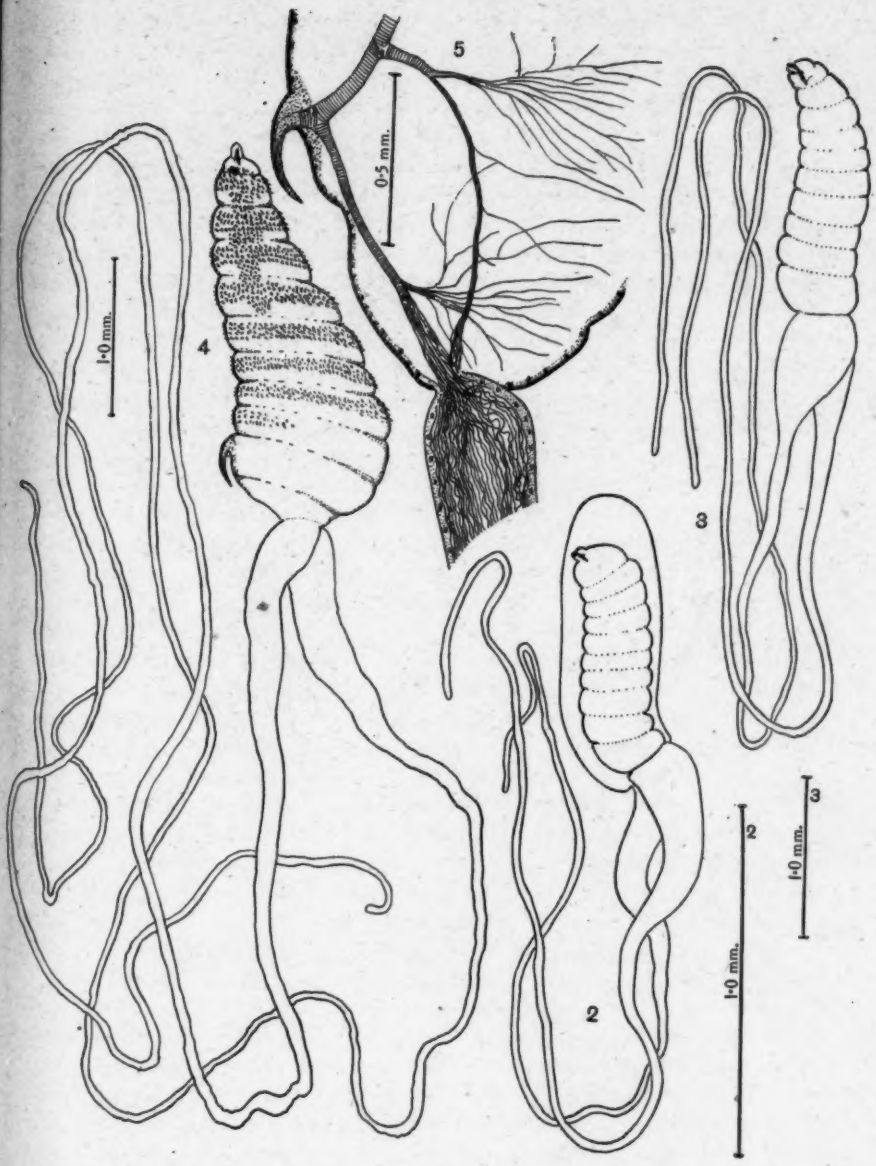


Fig. 2. *Cryptochaetum striatum*, Thorpe. Transition from first to second larval stages. First skin being cast.

Fig. 3. *Cryptochaetum striatum* Thorpe. Second larval stage.

Fig. 4. *Cryptochaetum striatum* Thorpe. Third larval stage.

Fig. 5. *Cryptochaetum striatum* Thorpe. Third larval stage, posterior region of the body to show posterior spiracle and tracheal supply of caudal process.

in its lack of cuticular spines and processes of any kind; the body is absolutely smooth. Details of the mouthparts are shown in Figs. 10 and 11.

Third-stage larva. This is illustrated in Fig. 4, and the outstanding point is of course the enormous development of the caudal filaments. They are now ten times the length of the body, sometimes more, and are packed with a great mass of fine tracheal branches which extend at least two-thirds of the way to the tip (Fig. 5). The body is now covered with short, stout, semi-transparent spines. Spiracles (Figs. 6, 7) are well developed, and on the whole resemble those of *Cryptochaetum grandicorne*. It will be seen that the anterior spiracles have the same resemblance to a hand with elongate fingers, the chief difference being that there are five fingers in the present species and only four in *grandicorne*. There appears to be a minute opening near the tip of each finger. Posterior spiracles are of the usual structure and need no comment. The mouthparts of the third-stage larva (Fig. 12) are particularly interesting. Whereas both *grandicorne* and *iceryae* have well-developed mandibles present in the third stage, in *striatum* they are represented only by a couple of pigmented and sclerotized plates embedded in the head, and apparently without musculature. Apart from the absence of mandibles, however, there are no very important differences. The dentate sclerite (*D*) is well developed and can presumably act as a rasp. This is probably quite sufficient to deal with the very soft diffuse fat body on which the animal feeds. During the earlier part of the third stage the larvae lie free in the body cavity, although they tend particularly to congregate in the region where there is a rich tracheal supply running to the wall of the egg pouch. The older third-stage larvae are found almost exclusively in the visceral chamber (Fig. 1, *V.*) where they are bathed in the blood which surrounds the digestive, reproductive and other systems and which is relatively free from fat body. Soon after taking up this position, it appears that the larvae thrust their posterior spiracles through the delicate wall separating the visceral cavity from the marsupium or egg chamber (*M*), thus bringing them into contact with the atmospheric air contained in the latter. Here they remain for the rest of the larval life, and while in this position it is doubtful whether they can reach much of the fat body on which they have up to now been feeding. It would seem that blood must again constitute the main food during this period.

As the larva prepares to pupate, a very remarkable change in form is noticed (Fig. 8). There is a steady contraction of the dorsal part of segments 4–8. As this proceeds it has the effect of bringing the anterior spiracles further and further backward until they come to lie quite close to the posterior ones. When this process is complete, the anterior spiracles are thrust through the same membrane as the posterior ones, and as soon as this happens, the hardening and pigmentation of the cuticle which mark the formation of the puparium proper take place rapidly. The result of the process, as will be seen from Figs. 8 and 9, is that the posterior and anterior spiracles finally come to lie in the same plane, namely, that of the puparial lid, which is now demarcated

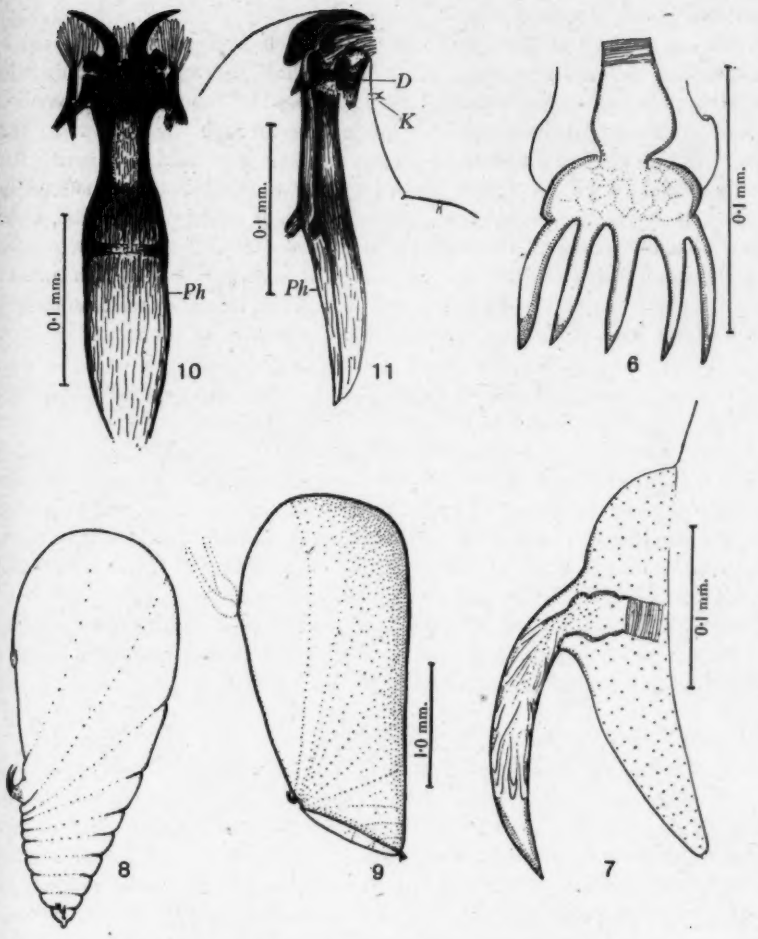


Fig. 6. *Cryptochaetum striatum*, anterior spiracle of third-stage larva.
Fig. 7. *Cryptochaetum striatum*, posterior spiracle of third-stage larva.
Fig. 8. *Cryptochaetum striatum*, change in form of third-stage larva prior to pupation.
Fig. 9. *Cryptochaetum striatum*, puparium.
Fig. 10. *Cryptochaetum striatum*, mouthparts of second-stage larva, dorsal view.
Fig. 11. *Cryptochaetum striatum*, mouthparts of second stage-larva, lateral view.

and which is formed from part of segments 1–3. This lid is of course flat and is pressed close up against the above-mentioned membrane. The dorsal parts of segments 4–8 are so contracted that they take up very little space indeed, so that the posterior spiracles are adjacent to the hinge region of the lid. Fig. 9 shows the relative proportions of the different body segments indicated by dotted lines in relation to the puparium as a whole. The whole transformation appears to be an admirable adaptation which enables the animal to have both its anterior and posterior spiracles projecting through the only membrane which is thin enough for them to pierce; and at the same time ensuring that the puparial lid will be closely pressed against the membrane, thus enabling the adult fly to emerge into the egg pouch. This it does in due course, and is then able to emerge to the exterior via the opening of the pouch without having to make its way through any region of thick cuticle. By this time the abdomen of the scale insect has begun to shrink and is usually raised somewhat above the bark, so that there is no difficulty in the parasite escaping. Soon after the puparium is formed, the caudal filaments wither and generally drop off.

As would be expected from the fact that parasitism by these insects does not usually take place until the host insect is about half-grown, a large number of individuals can come to maturity within one scale insect. What the limit is I am unable to say, but I have dissected two first-stage larvae, nine second-stage larvae, twenty-four third-stage larvae and twenty-eight puparia from a single host insect, thus making a total of sixty-three. It is of course improbable that all these individuals would have been able to come to maturity, for it is unlikely that after the emergence of the adults from the puparia the host would have been able to supply the nourishment required by the young larvae. Nevertheless, there is no doubt that a very considerable number of parasites may emerge from one host.

(*b*) Cryptochaetum tuberculatum *Thorpe.*

Cryptochaetum tuberculatum was found parasitizing a new species of *Aspidoproctus*, namely, *Aspidoproctus bifurcatus* Thorpe (1940), and it also attacks *A. glaber* Lindgr. which was present in the same locality. *A. bifurcatus* is smaller than *A. maximus* and is probably closely related to *A. armatus*, although it does not possess the striking spines which are characteristic of the latter form. It was first found at Kwamkoro, some few miles from Amani, on the bark of an introduced leguminous tree, *Inga vera*, and it was from this locality that the parasite was obtained. The scale was also common on *Cassia nodosa* at Amani, but I did not find it parasitized there.

This is not the place to describe the features of the adult parasite, for an account of which reference should be made to the accompanying paper (Thorpe, 1941). There are however many points of interest in connexion with the life history, which is, as will be seen, in striking contrast with that of *C. striatum*. In this case the female lays her eggs in the scale insects while they are still quite small, probably not later than the second instar, and development takes place in the

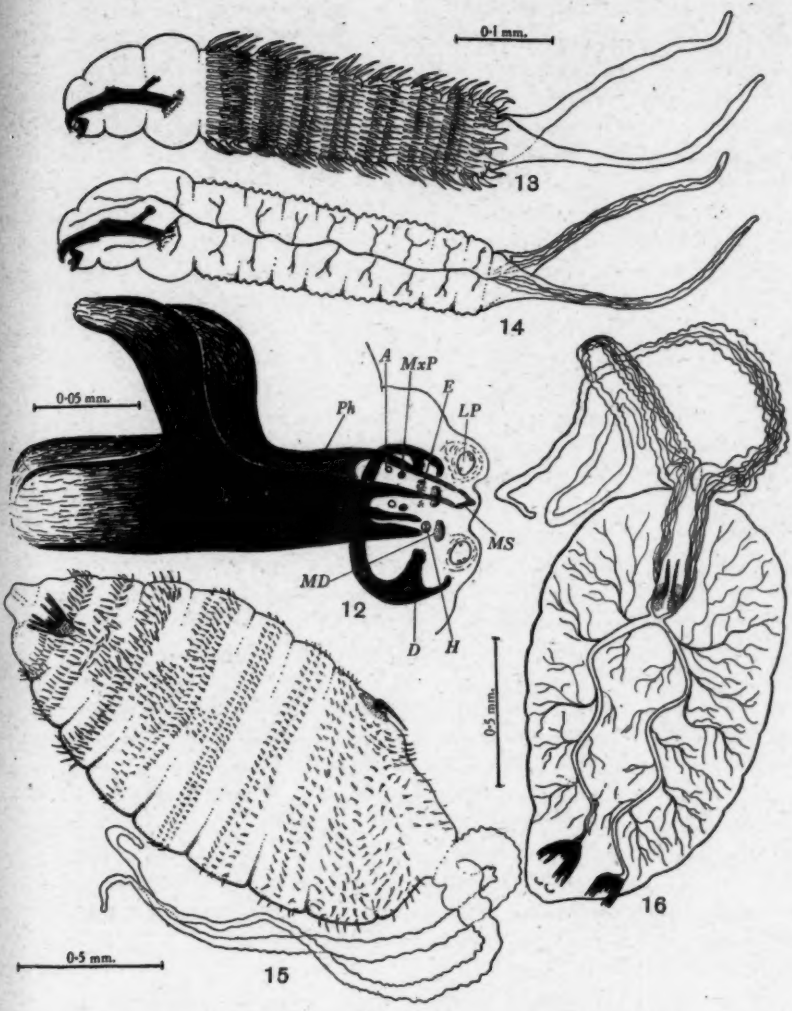
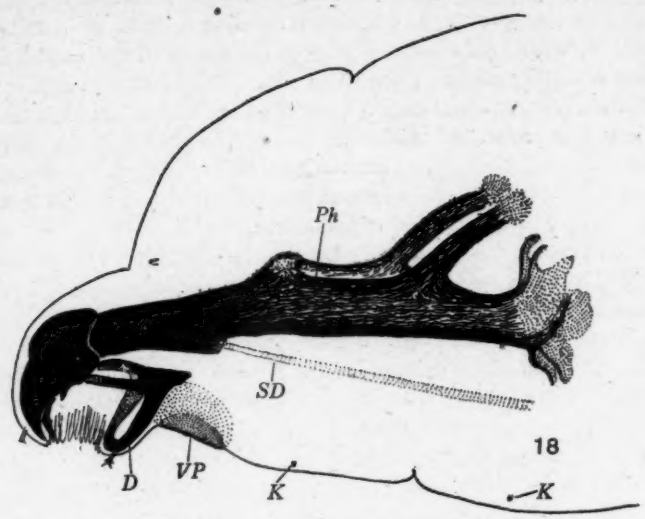


Fig. 12. *Cryptochaetum striatum*, mouthparts of third-stage larva.
Fig. 13. *Cryptochaetum tuberculatum*, second-stage larva.
Fig. 14. *Cryptochaetum tuberculatum*, second-stage larva to show main branches of tracheal system.
Fig. 15. *Cryptochaetum tuberculatum*, third-stage larva.
Fig. 16. *Cryptochaetum tuberculatum*, third-stage larva to show tracheal system.

body cavity in the usual way. I was not fortunate enough to find a first instar larva, but many examples of the second instar were studied, and as will be seen from the illustrations (Fig. 13) they are of a very characteristic appearance. The caudal filaments are short as compared to those of *striatum*, and contain a relatively poor tracheal supply (Fig. 14). More remarkable are the broad flexible filaments which beset the abdominal segments, the first few segments having four complete rings of these, the last two or three, three only. In this respect the second-stage larva is very much nearer to *C. iceryae* and *C. grandicorne* than is *striatum*. As will be seen from Figs. 17 and 18, the mouthparts are well developed and on the whole are similar to those of the second instar *striatum* and to corresponding stages of other members of the genus previously described. There are, nevertheless, many structural details which provide good diagnostic characters. The most peculiar feature of the mouthparts of this stage is the presence of a pair of rather irregular pigmented plates (*VP*) lying on the central part of the ventral surface, just behind the dentate sclerite. I am unable to assign any function to these, nor can I come to any conclusion as to what they represent. They appear to be embedded in the body wall, and I have not found any specific muscles attached to them. They are, however, very conspicuous, and provide an excellent means of identifying the larvae. The third-stage larva is again easy to distinguish from other forms. It has (Fig. 15) a considerable equipment of spines and the spiracles are well-developed and of characteristic form. The posterior ones (Figs. 20, 21), while of the same general shape as those of other species, are noteworthy for being unusually long and slender and for having a small protuberance covered with minute teeth just underneath the base. The anterior spiracles (Fig. 19) are of the hand-like type, each with twelve fingers, some of which are very long and slender. The caudal filaments are very short compared with *striatum*, being hardly longer than the body itself, and the tracheal supply (Fig. 16) is comparable with that found in *grandicorne*, only six to eight branches to each filament. The most noteworthy feature of all, however, is the complete absence of mouthparts. The pharyngeal trough is present, though only slightly pigmented, and is apparently normal in structure, but I could find no trace of anything else. In this character the species resembles *Cryptochaetum chalybeum*, described by de Meijere (1916).

When the third-stage larva is ready to pupate, it turns upside down in its host, the head of the larva pointing towards the posterior region of the scale insect. Shortly after the formation of the puparium the anterior spiracles are thrust through to the exterior. The caudal filaments are by this time cast off. Since by the time the parasite pupates the scale insect is still less than half-grown, it stands to reason that not more than a single parasite could come to maturity in any one host. As the scale insect is still young there is no difficulty about penetration of the cuticle by the spiracles. Consequently the change of form and the special adaptation which are characteristic of *striatum*, and which enable it to emerge into the marsupium, are not required and are

lacking. When the puparium (Figs. 22, 23) is fully formed the posterior spiracles are also projected through the body wall in the ventral region of the third thoracic segment between the bases of the legs, and by the time the



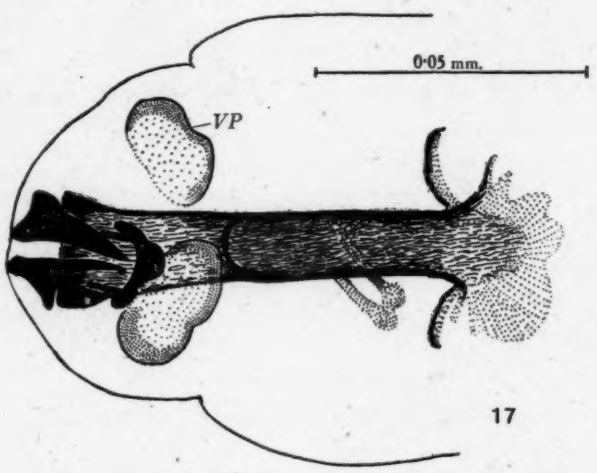


Fig. 17. *Cryptochaetum tuberculatum*, mouthparts of second-stage larva, ventral view.
Fig. 18. *Cryptochaetum tuberculatum*, mouthparts of second-stage larva, lateral view.

adult is ready to emerge the skin is dry and hard and of a papery consistency, and is adhering closely to the puparial lid. There is therefore no obstacle to the emergence of the adult.

(*c*) *Respiratory adaptation of* Cryptochaetum.

The writer has already shown (1931, 1934) that in two species of Cryptochaetum, *C. iceryae* and *C. grandicorne*, the caudal filaments act as tracheal gills. In this connexion one of the most striking features of *C. tuberculatum* as compared with *striatum* is the poor development of the caudal filaments and their relatively meagre tracheal supply. This of course is in line with the fact that the scale is small during the period of attack, and that there is no obstacle to the protrusion of the spiracles to the exterior quite early in the third larval instar. It is indeed interesting that such a close correlation can be observed between the degree of development of the tracheal gill system and the size of the host at the time of parasitism.

The existence of the exceedingly long caudal filaments of *C. striatum* raises an interesting problem, for it is obvious that, other things being equal, very long tracheal gills of this type must be less efficient per unit area than gills in the form of short broad flaps or processes distributed over the surface of the body. The long filamentous gill can only have the advantage, if, by reason of its length, it can be placed in contact with a region of higher oxygen tension and it is certainly noteworthy how often the caudal filaments of *C. striatum* are entangled among the tracheae of the host. But even so, increase in efficiency of the gill with increase in length must fall off very rapidly after a certain critical point has been reached. What this length is it is difficult to say with certainty, but let us assume for the sake of argument that the tail terminated in an open spiracle in contact with the atmosphere. We can then apply Krogh's well-known formula $S = k\frac{(p-p_1)a}{l}$. Where S = oxygen consumption of the animal in cubic centimetres per second; k = the diffusion constant for oxygen (0·18); a = the mean cross sectional area of the tracheae in cm.^{2}; l = the length of the tracheae in cm.; p = the partial pressure of oxygen in the atmosphere, and p_1 = the partial pressure of oxygen at the proximal end of the trachea. Assume an oxygen consumption at the average rate of 300 c.c. per kg. per hour. The average weight of a young third-stage larva is of the order of 0·002 g. so that $S = 16{\cdot}6 \times 10^{-8}$. The average diameter of the tail tracheae is 3μ and there are 40 in each tail so

$$a = 40 \times 2 \times \pi \times 1{\cdot}5^2 \times 10^{-8}.$$

The tracheae do not extend quite the full length so we can say $l = 0{\cdot}8$ cm. We thus get:

$$16{\cdot}6 \times 10^{-8} = 0{\cdot}18(p-p_1)\frac{40 \times 2 \times \pi \times 1{\cdot}5^2 \times 10^{-8}}{0{\cdot}8};$$

$\therefore\ p - p_1 = 0{\cdot}128 = 12{\cdot}8\%$ atmospheres, which indicates perhaps about the minimum degree of efficiency which can be regarded as satisfactory; being of the same order as some of Krogh's results with individual spiracles of the larva of *Cossus*. It is at any rate clear that if the caudal filaments were double

this length the additional 8 or 10 mm. would under these hypothetical conditions confer little or no advantage upon the larva. In other words, for the conditions postulated, the caudal filaments of *C. striatum* appear to have attained approximately their maximum effective dimensions.

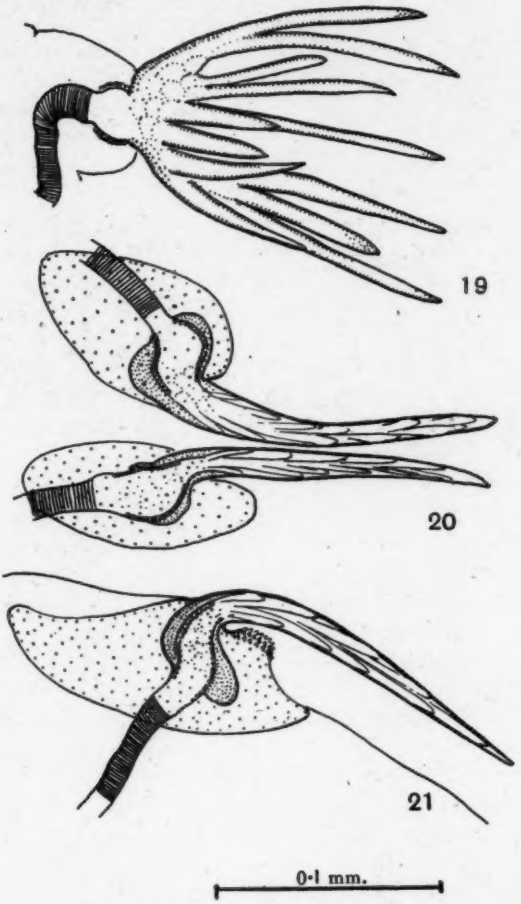


Fig. 19. *Cryptochaetum tuberculatum*, third-stage larva, anterior spiracle.
Fig. 20. *Cryptochaetum tuberculatum*, third-stage larva, posterior spiracle, dorsal view.
Fig. 21. *Cryptochaetum tuberculatum*, third-stage larva, posterior spiracle, lateral view.

Of course in actual fact the larva probably absorbs a considerable proportion of its oxygen requirement direct through its cuticle. It is probably therefore quite reasonable to assume that the caudal filaments have to provide for only about one-third of the total. In this event S would become $5{\cdot}5 \times 10^{-8}$ and the

resulting difference between p and p_1 would be 4%—a relatively high degree of efficiency.[1]

Wigglesworth (1939, p. 204) has suggested that perhaps the *main* function of the "tails" of various endoparasitic larvae and of the caudal vesicle of many Braconidae may be similar to that of the so-called "blood gills" of many

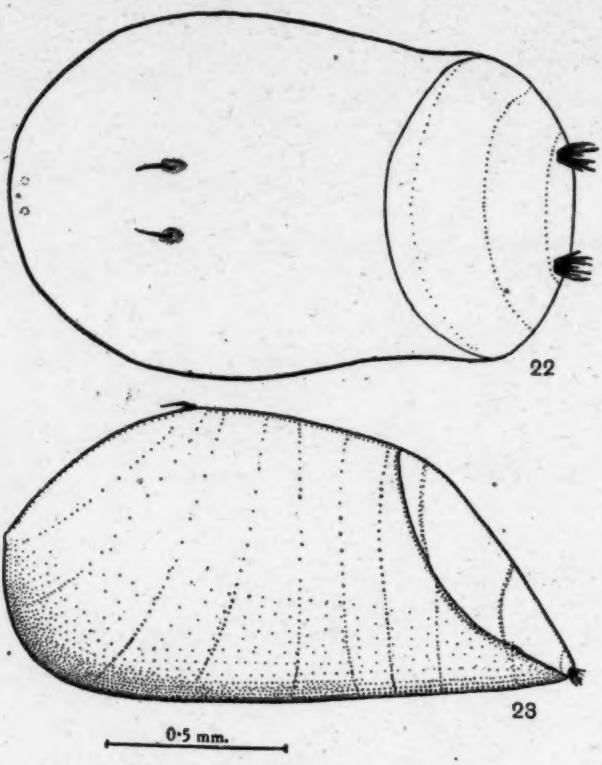


Fig. 22. *Cryptochaetum tuberculatum*, puparium, dorsal view.
Fig. 23. *Cryptochaetum tuberculatum*, puparium, lateral view.

aquatic larvae—namely absorption of water and salts. This explanation seems obviously inapplicable to the extreme case of *C. striatum*. Moreover, while organs of such function must clearly be important for larvae living in fresh water it is hard to see how they could be needed by an endoparasitic larva with closed hind gut, immersed in the blood of its host and feeding solely on blood and tissue.

[1] Similar calculations for *C. grandicorne* and *C. iceryae* give 7·2 and 14% respectively but I have not in these cases accurate weights of the larvae, so the results are not so reliable.

(ii) *Hymenoptera*

Eupelmus aspidoprocti *Ferrière.*

Besides *Cryptochaetum striatum*, another parasite, or rather internal predator, was also observed attacking *Aspidoproctus maximus*. It has been described for me by Dr Ferrière as *Eupelmus aspidoprocti* Ferrière. It is apparently a common species in East Africa, and I also found evidence of its work in Southern Rhodesia during my visit there later in the year.[1] The adult female Eupelmid was observed attacking a scale insect about 1 in. long which was attached to the trunk of a well grown specimen of *Albizzia stipulata*. The parasite was standing on the scale insect at about the middle region slightly to one side, with its head towards the margin. For about 2 min. it was palpating with its antennae. Then after some slight movements from side to side it sank its ovipositor deeply through the dorsal body wall of the scale about half-way between the lateral margin and the highest point, and slightly posterior to the middle region. The ovipositor was held in position for about 30 sec. to 1 min. The insect then withdrew and ran around on the bark nearby, shortly returning to the same scale. This behaviour was watched on more than one occasion, and females of the Eupelmid were kept in captivity and were given young *Aspidoproctus maximus* in different stages of growth in which to lay their eggs. The ovipositor apparently passes right through both the dorsal body wall, and the body cavity itself, into the marsupium of the host. This is presumably the reason for the careful way in which the egg-laying female chooses the exact point at which the egg is to be inserted. The long stalk of the egg (Fig. 24) probably also assists in the passage of the egg right through to the proper region. Perhaps the apex of the stalk is left protruding through the dorsal body wall, but I was never able to observe it.

A large number of eggs may be laid in one scale insect, and the larvae, which in general appearance are of the normal Eupelmid type, feed on the eggs and young scale within the pouch. They appear to be able to suck the juices of the young scale, the latter remaining attached to the head of the parasite larva until it has been sucked dry. If it is forcibly removed, the larva continues sucking and swallows air. The mouthparts are shown in Fig. 25. The only noteworthy point about them is the absence of the serrated clypeal or labral ridge described for mature larvae of *Eupelminus* (McConnel, 1918), *Eupelmella* (Morris, 1938), and *Eupelmus allynii* (Phillips & Poos, 1921). This may perhaps be accounted for by the fact that it feeds on eggs and does not require the mouth equipment capable of dealing with active and well-grown larvae. Little need be said about the structure of the larval body. There are twelve distinct segments behind the head, numbers 2–10 inclusive bearing a pair of spiracles. Each of the twelve segments is marked by a single ring of

[1] Through the kindness of Mr Melville of the Scott Agricultural Laboratories, Nairobi, I have since received specimens of larvae apparently of this species parasitizing *Aspidoproctus glaber*, and possibly *A. pertinax* also, at Maseno, Kenya.

rather widely spaced bristles. The fully grown larva measures about 6 mm. in length. On completion of feeding the host insect is generally moribund, and the larva forms a rather viscid brown cocoon among the debris of the eggs

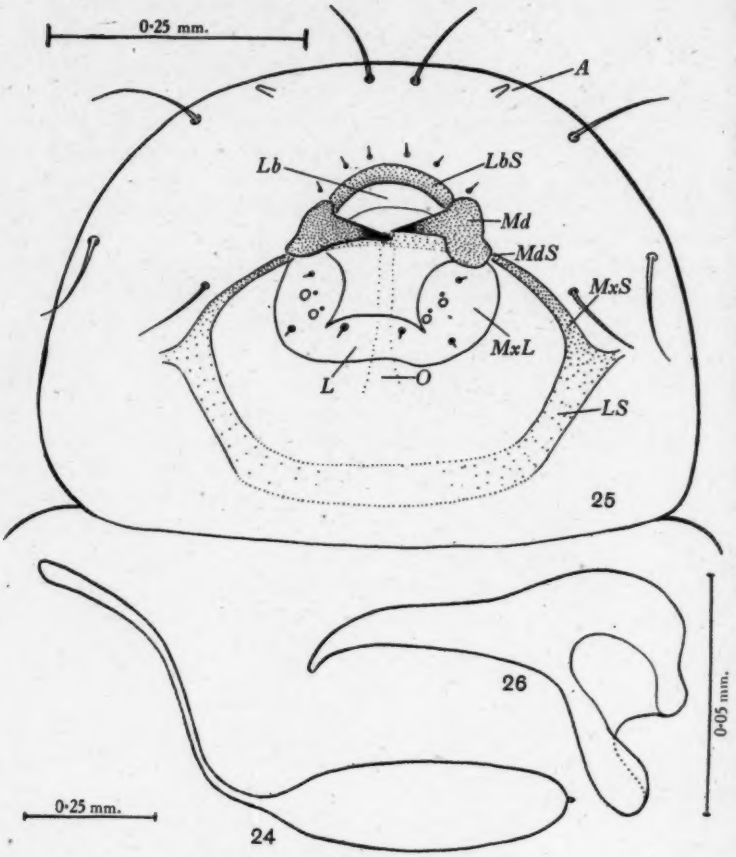


Fig. 24. *Eupelmus aspidoprocti* Ferrière, ovarian egg.
Fig. 25. *Eupelmus aspidoprocti* Ferrière, mature larva, head and mouthparts, ventral view.
Fig. 26. *Eupelmus aspidoprocti* Ferrière, mature larva, right mandible, internal view.

and young scales and pupates. The adult on emergence does not take advantage of the natural exit used by *Cryptochaetum*, but cuts a neat round hole in the dorsal or ventral body wall and thus makes its way to the exterior.

4. SUMMARY

1. The larvae of those Diptera and Hymenoptera which develop as endoparasites in scale insects often show striking respiratory and other adaptations correlated with the degenerate structure and organization of the host. The larger the host the more acute must be the problem of respiration.

2. *Aspidoproctus maximus* is a very large Monophlebine scale insect infecting trees and shrubs of the order Leguminosae in tropical and subtropical East Africa from Kenya to Southern Rhodesia. The main anatomical and biological features are described, including the very hard and thick dorsal body wall, the large invaginated marsupium in which the eggs are hatched and the adaptation of the young for wind dispersal.

3. *Cryptochaetum* (Diptera, Agromyzidae) is a genus of highly specialized parasites attacking monophlebine scale insects throughout the world. A new species *C. striatum* was discovered attacking *Aspidoproctus maximus*. The body wall of the well-grown host is pierced by the ovipositor of the fly and the eggs are placed in numbers in the haemocoel. The larvae feed on the blood and fat body of the host. As they grow they develop to a quite extraordinary degree the respiratory caudal processes which are so characteristic of the genus. These float in the blood of the host and act as tracheal gills. They are often entangled among the host's tracheae. In the third instar they are packed with fine tracheal tubes and may be ten times the length of the body of the larva.

4. The question of the maximum effective length of gills of this form is discussed and Krogh's formula is applied. It appears doubtful whether any further increase in length would be accompanied by any increase in efficiency.

5. The thickness of the host's dorsal cuticle presumably renders emergence in the normal manner impossible. Instead, the insect pupates with its spiracles penetrating the thin membrane separating the haemocoel from the marsupium. The fly thus emerges into the marsupium and makes its way to the exterior by the same route as the newly hatched scales themselves.

6. By contrast the life history of another new species of *Cryptochaetum*, namely, *C. tuberculatum*, is described. This lives as a solitary endoparasite in the *young stages* of *Aspidoproctus bifurcatus* and *A. glaber*. It has therefore no special difficulties of respiration and emergence to overcome and it is interesting to find that its caudal processes are much shorter and contain relatively few tracheae and that its mode of pupation is normal.

7. The life history of *Eupelmus aspidoprocti*, a new Eupelmid parasite of *Aspidoproctus maximus*, is also described. The stalked egg is inserted through the body wall into the cavity of the marsupium where the larvae live devouring the developing eggs and young. Pupation takes place within the host and the adult eats its way out dorsally.

Lettering of figures

A	antenna	*MdS*	mandibular strut
An	anus	*MS*	median dorsal sclerite
Ap	aperture of marsupium	*MxL*	maxillary lobe
D	dentate sclerite	*MxP*	maxillary palp
E	epipharyngeal plate	*MxS*	maxillary strut
F	fat body	*O*	œsophagus
H	hypopharyngeal plate	*Op*	operculum
K	Keilin's sense organ	*P*	puparium of parasite
L	labial lobe	*Ph*	pharyngeal sclerite
Lb	labral region	*S*	supra visceral membrane
LbS	labral strut	*SD*	salivary duct
LP	labial palp	*T*	trachea
LS	labial strut	*V*	visceral cavity
M	marsupium or brood pouch	*VP*	ventral plate
Md	mandible		

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A NEW COCCID-PARASITE OF THE FAMILY EUPELMIDAE (HYM. CHALC.)

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We received from Dr W. H. Thorpe a remarkable Eupelmid bred from the large Coccid, *Aspidoproctus maximus* Newstead, in East Africa. As Dr Thorpe has been able to make some interesting observations on the life history of this parasite, I have been asked to study it specially. It differs from all other known species of *Eupelmus* from Africa, and I am giving here a description of that species.

Eupelmus aspidoprocti n.sp.

♀. Body black, with dark greenish and violaceous reflexions, specially on head, pronotum and mesopleurae. Antennae with scape and joints 2–5 of funicle yellow, the rest black. Front and hind legs black, tip of tibiae and tarsi orange-yellow; middle legs with the femora except at tip, the tibiae except at base and joints 3–5 of the tarsi orange-yellow; middle and hind knees with white spots. Wings entirely infuscate, except a transverse hyaline area at about the middle of the submarginal vein. Ovipositor sheaths yellow, with only the extreme base black.

Head, seen from the front, a little broader than high; eyes large, oval, with short and weak ciliation; frons broad, the lateral ocelli farther distant from each other than from the front ocellus. Antennal furrows well marked but not very deep, the sides sharply margined and converging above, reaching almost the front ocellus. Face, cheeks and frons dull, finely punctate and reticulate. Vertex narrow, but not carinated, behind. Antennae inserted a little below the lowest level of the eyes; scape narrow, not reaching to the front ocellus; pedicel narrow and elongate, somewhat longer than the third of the scape; annellus subquadrate; 1st funicle joint shorter than the pedicel, about twice as long as broad; the following joints gradually shorter and broader, the 5th quadrate, the 6th and 7th broader than long; club a little longer than the two preceding joints together and sharply truncate above.

Thorax weakly, but densely punctate. Mesonotum concave behind, the middle basal elevation oval, narrowing behind, the side elevations sharply carinated before the hind margin; the sides of the mesonotum with some scattered white scale-like ciliae. Scutellum short, rounded behind, rather narrow in front, with some long black ciliae at base, intermixed with a few white broadened ciliae. Mesopleurae densely and finely reticulate, more shagreened near the middle. Front legs with the femora much broadened towards the tip, the tibiae short, the tarsi longer than the tibiae; middle legs

elongate, metatarsus broad with black spines below; hind legs with the femora slightly broadened, the tarsi elongate, as long as the tibiae. Wings broad, reaching beyond the tip of the abdomen, densely ciliate; stigmal vein rather long, curved, scarcely knobbed at tip, as long as the postmarginal vein, each about as long as the third of the marginal vein.

Abdomen short oval, as long or slightly longer than the thorax, but broader, depressed above; 1st segment broader than long, deeply incised behind, the following segments short and not emarginate. Ovipositor as long as the hind tibiae.

♂. Head and thorax with green, blue and violaceous reflexions, abdomen aeneous; antennae black, scape yellow; legs black with metallic reflexions, front tibiae, end of middle and hind tibiae and three first joints of the tarsi yellow; middle and hind knees with weak white spots. Wings hyaline.

Head and antennae similar to those of the female, the scape a little broader, the flagellum somewhat shorter. Thorax normal, parapsidal furrows narrow and complete; scutellum large, longer than broad; propodeum almost smooth, with a median carina. Abdomen oval, shorter and not broader than the thorax.

Length: ♀ 4 mm.; ♂ 3 mm.

Tanganyika Territory, Amani, 4 ♀ 1 ♂, 24. iii. 1939 (Dr W. H. Thorpe). Ex *Aspidoproctus maximus* Newstead.

The rather short and broad abdomen, where only the first segment is incised behind, the shortly carinated scapulae, the strongly margined antennal furrows, which extend upwards to the front ocellus, and the relatively long stigmal vein show that it is not a typical *Eupelmus*. It is however difficult to place it with certainty in any other known genus and as long as a revision of numerous species described in *Eupelmus* and of Eupelmid genera has not been made, it is better to accept the genus *Eupelmus* in a broad sense.

We have, however, compared *E. aspidoprocti* with the genotypes of some other genera which are or may seem related to it.

Lutnes ornaticornis Cam., from Central America, is the most closely related with its short abdomen, darkened wings, coloured antennal joints and strongly margined antennal furrows. But the first abdominal segment is distinctly longer than broad although not as long as the other segments united as Ashmead says; the antennal furrows are broader, shorter and deeper, and do not reach as high as the front ocellus; the eyes are more closely ciliate; the wings have a transverse hyaline band under the marginal vein, interrupted in the middle, as in some *Anastatus* spp.; the stigmal vein is much shorter, as is also the ovipositor and the tarsi.

In Ashmead's key of genera, our species would best run to *Idoleupelmus*. The type of *I. annulicornis* Ashm. from the West Indies, which is in the British Museum, differs however greatly by its smooth head with more converging eyes and smaller antennal furrows and by its much smaller size.

Bruchocida vuilleti Crawf., an African species, has also white scale-like

ciliae, but they are more widely distributed on head, thorax, and sides of abdomen. The antennal furrow is short, not marginated, far from the front ocellus; the abdomen has the four first segments emarginate.

Lecaniobius cockerelli Ashm., another Eupelmid parasite of scale insects, has a quite different form of head and its abdomen is without protruding ovipositor.

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STRUCTURE OF *HEMIMERUS DECEPTUS* REHN. VAR. *OVATUS*; AN EXTERNAL PARASITE OF *CRICETOMYS GAMBIENSE*

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(With 29 Figures in the Text)

Introduction

Hansen (1894) was the first to describe the external anatomy of *Hemimerus*, which he called *H. talpoides*. Jordan (1909) gave a general description of the internal anatomy of this animal. Heymons (1909) presented an exhaustive monograph dealing with the development of *Hemimerus*, especially in relation to the genitalia.

During my studies on the structure and systematic position of *H. deceptus* Rehn, var. *ovatus*, I have found some significant features in the external anatomy which seem to be correlated with its supposed parasitic life. These features are the modifications in the mouthparts, body segments and the thoracic legs.

This paper narrates these modifications with suitable figures. The rest of the anatomy and the systematic position of *Hemimerus* form the basis of a separate paper. The technical terms adopted in this work are based on Imms (1936), Snodgrass (1935), Rehn (1936), and Crampton (1918).

Host association and distribution

The material was gathered from farmhouse rats in Tanganyika territory. The rats were identified as *Cricetomys gambiense*, and the insects were collected from the flank regions of the rats.

Hemimerus was thought to be an ectoparasite of this rat as early as 1890, and subsequent authorities maintain that *Hemimerus* is an ectoparasite (Rehn, 1936).

I have found the following substances in the gut contents of a number of specimens: fungal spores, epidermal scurf, some amorphous white material, and some dark clots. If *Hemimerus* is an ectoparasite of this rat its food will be the bits of skin, hairs, and perhaps blood. From the size of the insect one can say that if it took this diet continuously, there would be no hairs left on the skin of the rat. Rodent skins are often infested with fungi which cause the hairs to fall, and thus leave patches of bare skin. The spores found in the gut contents of *Hemimerus* have not yet been identified. Innumerable mites were

recovered from the intersegmental membranes of the terga and sterna, as well as the genital orifices of many specimens. These have been identified as the hypopus stages of a Tyroglyphid mite.

Thus the rat *Cricetomys* seems to tolerate the presence of *Hemimerus*. Jordan (1909) had indicated the possibility of the same kind of relationship.

Distribution. In his survey of this insect in South Africa, Rehn (1936) has recorded specimens belonging to the divisions *bouvieri* and *vossleri*, from the Usamba mountains of Tanganyika territory. The present specimens were collected in the Morrogoro region of Tanganyika. They have been identified as the species *deceptus* which, according to Rehn (1936), has been found in Pretoria, Transvaal. Thus the distribution of *Hemimerus deceptus* extends from the south of Africa to Tanganyika.

EXTERNAL ANATOMY

Head

The head is prognathous, flattened dorso-ventrally, and expanded laterally. Beyond the occipital suture, the posterior region is drawn in, so that the anterior part of the prothoracic tergum lies partly covered by the head. The anterior part is semicircular and carries at its apex the labrum, and the maxillary palps. The antennae are situated in depressions on the sides of the head.

There is no indication of sutures on the dorsal surface of the head, except for the suture that separates the labrum from the clypeus. At the sides of this suture lie the bases of the mandibles. There is no fronto-clypeal suture, and the frons can only be located by the attachment of the muscles in that region. Starting from the base of the mandible, a faint line, marking a slight depression, runs in a loop. The region posterior to this line may be considered as frons, and that anterior to it as clypeus.

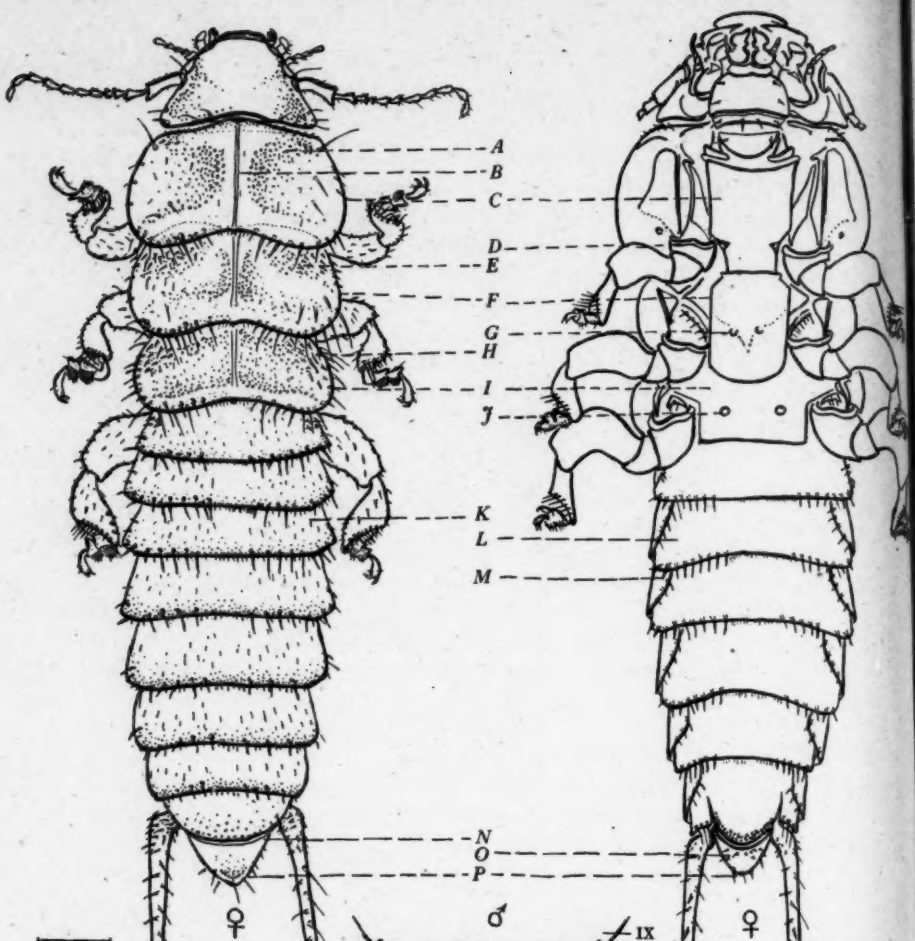
Antenna

The antennal sutures lie at the sides of the head. The depression (Fig. 22 *C*) on the ventral side of the head hides the scape (*D*), while the rest of the antenna lies on the underside of the protergum. The flagellum (*G*) consists of nine filiform joints, all of which bear disto-laterally fine sensory pits. In young insects the flagellum has only six segments.

Mouthparts

Labrum (Fig. 6). The labrum is a crescentic plate in the anterior part of the head. Small hairs are present on the fronto-lateral border. At the postero-lateral angles the labrum bears a small pair of curved sclerites, which are the tormae (*A*) (Snodgrass, 1935).

Maxilla (Fig. 8). The cardo (*M*) bears a condyle (*N*) that articulates with a hinge in the submentum. The stipes (*K*) is supported on the cardo by two small peg-like joints (*L*). On the outer side of the stipes lies the palpifer



Figs. 1–3. Showing the entire body of *Hemimerus*.

Fig. 1. Female *Hemimerus* as seen from the dorsal side (drawn to scale). *A*, *E*, *H*, lateral depressions of the pro-, meso- and metathorax; *B*, median longitudinal groove; *C*, prothorax; *F*, *I*, meso- and metathorax; *K*, tergum of the abdomen; *N*, epiproct; *P*, tip of the abdomen or telson.

Fig. 2. The terminal portion of the abdominal region of a male specimen of *Hemimerus*, as seen dorsally (drawn to scale). *Q*, parameres; IX, X, XI, 9th, 10th, and the 11th terga.

Fig. 3. A female specimen of *Hemimerus*, as seen from the ventral side. Hairs and setae are not drawn (semi-diagrammatic). *F*, *I*, meso- and metathoracic sterna; *D*, prothoracic sternocostal pits; *J*, metathoracic sternocostal pit; *L*, abdominal sternum; *M*, postero-lateral prolongation of the tergum; *O*, paraproct.

carrying a five-jointed maxillary palp (*E*). At the base of the palpus is an oval membraneous sensory area (*I*) with a thick setae. The tip of the last palpal joint bears a sensory papilla. The lacinia and galea have separate articulations and move independently of each other.

The lacinia (*D*) has the form of a folded sheet, whose top slopes down on one side. The fold is incomplete on the inner side, and from inside the fold arise about a dozen sickle-shaped hooks (*H*). The galea (*C*) is a stout, single-jointed lobe bearing setae on its inner side. Anteriorly it bears an elliptical area covered by a thin transparent membrane studded with minute hairs, which are presumably sensory (*A*).

Mandible (Fig. 7). The mandible which is triangular articulates with the cranium on its ventral side by a condyle-like bulla (*F*), and on its dorsal side by the groove-like ginglymus (*E*). Each mandible bears two incisor teeth directed upwards. At the inner posterior side of the mandible lies the "prostheca" which has a few minute hairs directed towards the buccal region.

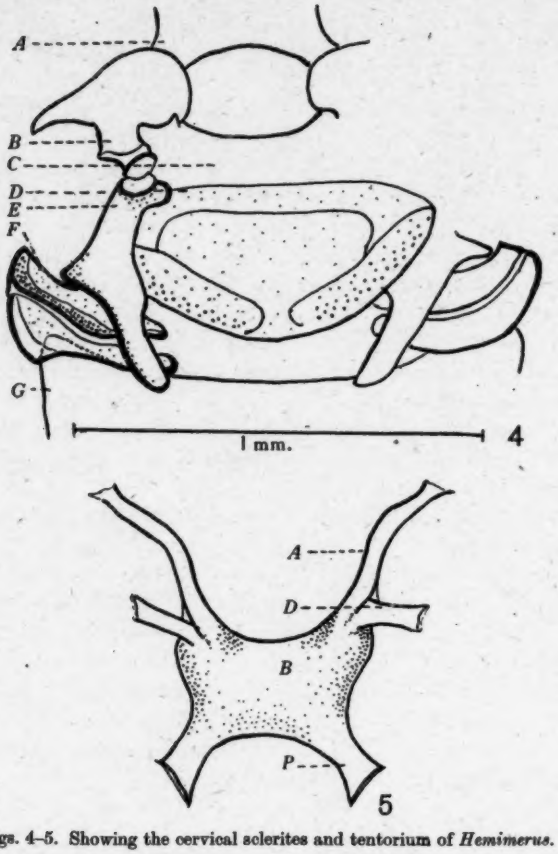
Labium (Fig. 9). The entire floor of the prognathous head is occupied by the labium. Anteriorly the labium consists of a membranous ligula (*B*) studded with minute hairs. The labial palp is three-jointed, and the last joint carries a small sensory papilla at the tip. The inner sides of the rectangular base of the ligula are sclerotized (*D*) to form a supporting plate for the base of the ligula. This plate meets the incurved rods of the suspensoria of the hypopharynx lying below the ligula.

Behind the ligular base is a semi-sclerotized area which is the mentum (*E*). Posterior to this is the submentum (*F*), which is the biggest sclerite and forms a concave arc posteriorly. The gula follows the submentum which, owing to the prognathous condition of the head, seems to be buried inside the head. The post-occipital region of the head curves inwards to meet the short hypostomal bridge. A cavity is thus formed which has the rim of the occipital suture as its projecting roof. The posterior margin of the gula is the lower limit of this cavity. The anterior part of the prothoracic tergum lies inside this cavity and is covered by the projecting rim of the occipital suture. The bases of the occipital condyles lie half inside the gular area, only the terminal part of each condyle being visible. The posterior tentorial arms meet the bases of condyles on the dorsal side of the submentum.

Hypopharynx and superlinguae

The hypopharynx (Fig. 10, i, ii) is conical and carries dorso-laterally two hollow pinnae-like superlinguae (ii, *H*). The dorsal surface of the hypopharynx is membranous and beset with minute spines, while a large part of the posterior ventral surface is sclerotized (*B*). There are two small depressions on the anterior region of the dorsal surface (*F*), and similar depressions, as well as spines, are present on the superlinguae. The sides of the superlinguae are strengthened by a pair of sclerotized rods (ii, *I*), while the hypopharynx bears a pair of sclerotized rods at the ventral side (i, *C*), and an unpaired curved rod

at the dorsal base (*J*). All these rods rest on the three-branched suspensorial sclerite. The posterior branch of this sclerite is thickened, and bears a thin membrane to which are attached groups of muscles (*O*). Hansen (1894) considered this area to be full of sensory pits. The inner arm (*L*) supports the



Figs. 4–5. Showing the cervical sclerites and tentorium of *Hemimerus*.

Fig. 4. Cervical sclerites as seen from the ventral side (drawn to scale). *A*, posterior arm of tentorium; *B*, right occipital condyle; *C*, membranous area between the gula and the ventral cervical sclerite; *D*, ventral cervical sclerite; *E*, lateral cervical sclerite; *F*, transverse cervical sclerite; *G*, first thoracic sternum.

Fig. 5. The tentorium (drawn to scale). *A*, anterior arm of the tentorium; *B*, body of the tentorium; *D*, dorsal arm of the tentorium; *P*, posterior arm of the tentorium.

above rods, while the outer arm (*M*) bends down towards the base of the ligula to meet the transverse sclerite lying below it. A complete ring is thus formed within which the hypopharynx lies. The dorsal region of the hypopharynx is continuous posteriorly with the floor of the buccal cavity, and the

hollow of the hypopharynx is traversed by muscles and a nerve from the sub-oesophageal ganglion.

Tentorium

The anterior arms of the tentorium are slender and long (Fig. 5 *A*), and curve laterally to articulate with the cranium behind the mandibles. The dorsal arms arise near the bases of the anterior arms and extend dorso-laterally to join the cranium (*D*). The posterior arms (*P*) are short and meet the cranium behind the occipital condyles. The body of the cranium is concave ventrally.

Thorax

Terga (Figs. 1, 3). The thoracic sclerites occupy nearly half the length of the trunk region of the insect. The prothoracic segment is the biggest and the metathoracic is the smallest.

The prothoracic tergum (Fig. 1 *C*) is nearly twice as broad as long. The antero-lateral margins have slight depressions (*A*), which bear thick, short, forwardly directed setae. The concave posterior margin overlaps the tergum of the mesothorax, and bears a row of setae. The entire segment is sparsely covered with minute hairs.

The mesothoracic tergum is twice as broad as long, and laterally bears two depressions (*E*) which are studded with thick setae directed postero-laterally. The posterior border covers the metatergum, and bears a row of setae.

The anterior margin of the metathoracic tergum is blunt and curved, and the antero-lateral depressions (*H*) contain backwardly directed setae which are more numerous than those in the pro-, and mesothorax. The posterior margin covers the anterior region of the abdominal segments.

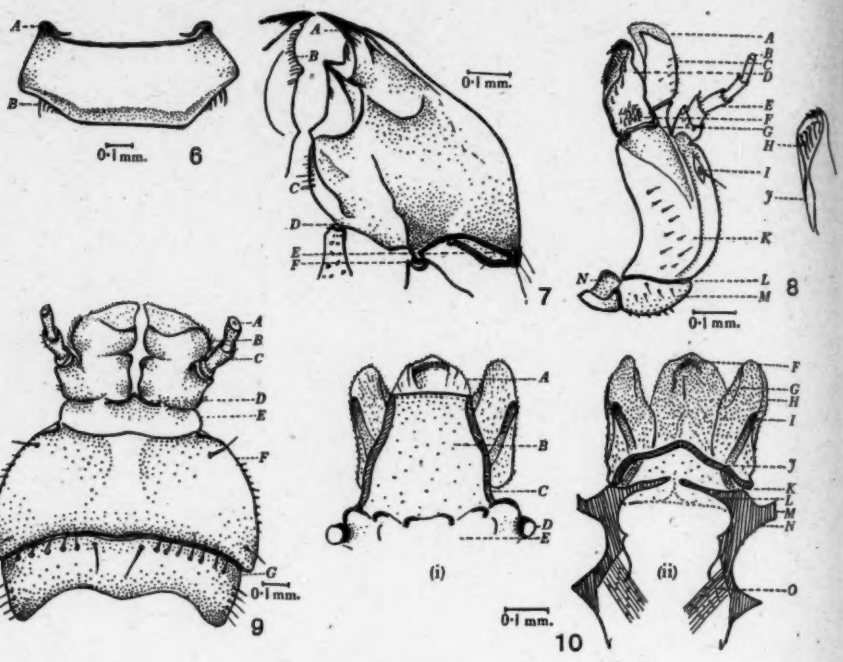
Sterna (Figs. 3, 12). The sternum of the prothorax is shield-shaped (Fig. 12 *F*). The posterior margin partly overlaps the anterior margin of the meso-thorax. Half way down each side are the marks of the sterno-costal pits (Fig. 2 *H*).

The sternum of the mesothoracic segment is longer than broad, and is rounded posteriorly where it overlaps the anterior part of the metathorax. The sternocostal pits are more prominent (*N*), and the entire surface of the sternum is covered with thin hairs and some setae.

The sternum of the metathorax (Fig. 3 *I*) is broader than long, and the anterior surface is expanded laterally. The sternocostal pits (*J*) are deep, and the posterior margin covers the first abdominal sternum.

The sternal apophyses (Figs. 13–15). The posterior-lateral sides of the pro-thoracic sternum (Fig. 13) are curved in (*E*), and on the knobs of the sterno-costal pits (*D*) rest the curved sternal apophyses (*B*). Anteriorly each apophysis is connected with the pleural ridge (*C*), and is prolonged beyond it.

On the mesothorax (Fig. 14) an internal transverse ridge—the sternocosta—lies on the dorsal surface of the eusternum. The median region of this ridge forms the furca (*C*). From the central part of this ridge arises a backwardly



Figs. 6–10. The mouthparts of *Hemimerus*.

Fig. 6. Labrum (drawn to scale). *A*, tormae; *B*, sensory hairs.

Fig. 7. Mandibles as seen from the ventral side. Only the right one is shown completely (to scale). *A*, incisor tooth; *B*, furrowed area in the anterior dorsal region of the left mandible; *C*, prostheca; *D*, muscle attaching area; *E*, ginglymus; *F*, bulla.

Fig. 8. The right maxilla as seen from the ventral side of the animal. There is a small diagrammatic representation of the anterior region of the lacinia (the maxilla is drawn to scale). *A*, sensory area of the galea; *B*, sensory papilla on the tip of the palp; *C*, galea; *D*, lacinia; *E*, maxillary palp; *F*, sensory spot with roots of hairs; *G*, subgalea; *H*, sickle-shaped hooks of the lacinia; *I*, sensory area; *J*, curved margin of the lacinia; *K*, stipes; *L*, place of articulation of the cardo with the stipes; *M*, cardo; *N*, articulation with the cranium condyle.

Fig. 9. The labium as seen from the ventral side of the animal (drawn to scale). *A*, sensory area of the tip of the labial palp; *B*, ligula; *C*, labial palp; *D*, chitinized base of the ligula; *E*, mentum; *F*, submentum; *G*, gula.

Fig. 10. Dorsal (ii) and ventral (i) views of the hypopharynx (drawn to scale). *A*, membraneous anterior part of the ventral side of the hypopharynx; *B*, chitinized posterior part of the ventral side of the hypopharynx; *C*, ventro-lateral rod of the hypopharynx; *D*, ventral prolongation of the suspensorial sclerite; *E*, base of the hypopharynx; *F*, *G*, depressions in the hypopharynx and the superlingua; *H*, superlingua; *I*, sclerotic rod in the superlingua, at its side; *J*, dorsal sclerotic rod of the hypopharynx; *K*, ventro-lateral rod of the hypopharynx; *L*, *M*, *N*, different branches of the suspensorial sclerite of the hypopharynx; *O*, muscles at the base of the suspensorial sclerite.

directed, free, truncate, sclerite (*E*), which has a small median slit. The fixed ends of the ridge (*B*), bear the endosternite of the mesothorax (*A*). This endosternite, or the apophysis, extends laterally to meet a triangular elevation (*D*) on the pleural ridge of its side.

Each endosternite of the metathorax (Fig. 15 *D*) is flattened and is situated near the margin on the deep sternocostal pits (*E*) of the eusternum. It is fan-like and the arms of the endosternum form muscle attachments.

Pleurites (Fig. 11). There are three main pleural sclerites in the thorax. The first is the trochantin (*E*, *O*, *W*) of which the shape and size varies in the three segments. It is biggest in the prothorax (*E*), and smallest in the mesothorax (*O*). The second is the episternum (*D*, *N*, *T*), which articulates with the tergum (*A*) and the trochantin in the prothorax, but only with the tergum in the metathorax. The third is the epimeron (*C*, *M*, *V*), which articulates jointly with the episternum (*D*), and tergum in the prothorax. It forms the pleural suture (*G*, *P*, *X*) in all the segments by union with the outer sides of the episternum (*D*, *N*, *T*), and is smallest in the metathorax.

Cervical sclerites (Fig. 4). There are five supporting sclerites in the neck region. The lateral (*E*), and the transverse (*F*) sclerites are paired; while the ventral sclerite (*D*) is unpaired.

The lateral sclerite articulates anteriorly with the occipital condyle (*B*), and posteriorly it becomes broader. The outer side of this broad area rests upon the transverse sclerite (*F*), while the inner side projects freely into the prothorax. The transverse sclerite is folded and this folding serves as a lever. Between the gula and the sternum of the prothorax, lies the ventral sclerite, which is triangular in shape, with the apex of the triangle directed posteriorly. The angles are rounded and stout setae arise from the strongly sclerotized rim. A thin membrane (*C*) lies folded between this sclerite and the posterior part of the head.

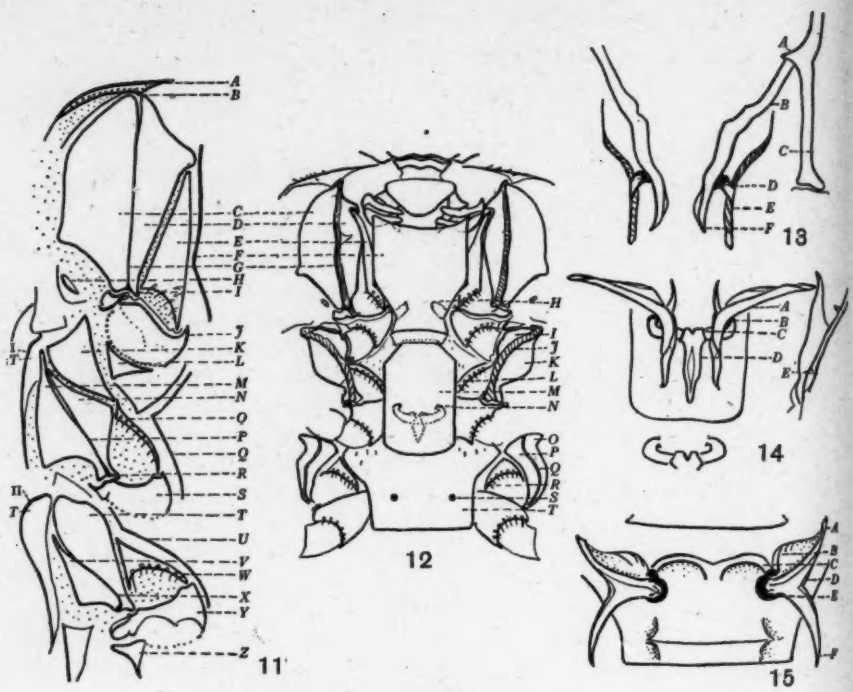
Thoracic appendages

These exhibit modifications associated with the semiparasitic habitat (Figs. 16–21). The three pairs of legs increase in size from the first to the third, and are situated at the sides of the sternum.

Proximally the coxea (Fig. 20 *C*) is thickened and bears a basicostal suture and ridge which is best seen dorso-laterally in the first pair of legs. The meron is also more visible in the first pair of legs. The coxa articulates with the pleuron by two grooves. The inner groove is near the end of the trochantin, while the outer groove is near the meron. The distal margin of the coxa is marked by a row of stout bristles.

The trochanter (Fig. 20 *F*) is the smallest segment of the leg. Inside the coxa are two small grooves and the trochanter articulates with the coxa by small pegs which move in these grooves. The femoral articulation consists of a double ball-and-socket joint (Fig. 16).

The femur (Fig. 20 *J*) is the largest segment of the leg, is convex anteriorly and concave posteriorly. Distally there are two sclerotized prolongations



Figs. 11–15. Showing the thoracic sternites, pleurites, and the sternal apophyses, of *Hemimerus* (all diagrammatic).

Fig. 11. The left thoracic pleurites. *A*, tergum of the prothorax; *B*, place of the articulation of the pleuron with the tergum; *C*, *M*, *V*, epimeron of the pro-, meso-, and metathorax, respectively; *D*, *N*, *T*, episternum of the pro-, meso-, and metathorax respectively; *E*, *O*, *W*, trochantin of the pro-, meso-, and metathoracic pleuron respectively; *F*, prothoracic sternum; *G*, *P*, *X*, pleural suture of the pro-, meso- and metathoracic pleuron; *H*, first spiracle; *I*, *R*, ridge of the pro- and mesothoracic pleurites, that articulates with the coxae; *J*, *S*, *Y*, coxa of the first, second, and the third pair of legs; *K*, *L*, post-coxal bridge of the prothoracic pleuron; *Q*, mesothoracic sternum; *U*, metathoracic sternum; *Z*, post-coxal bridge of the metathorax; (I), (II) the terga of the meso- and metathorax.

Fig. 12. All the ventral thoracic sclerites. *C*, *D*, *E*, *F*, *G*; these letterings are common with those of Fig. 11. *H*, sternocostal suture of the prothorax; *I*, *P*, episternum of the meso- and metathorax; *J*, *Q*, pleural sutures of the meso- and metathorax; *K*, *O*, epimeron of the meso- and metathorax; *L*, *R*, trochantin of the meso- and metathorax; *M*, *T*, meso- and metathoracic sterna; *N*, *S*, sternocostal pits of the meso- and metathorax.

Fig. 13. The sternal apophyses of the thorax, with the tergum removed (*prothorax*). *A*, the pleural articulation with the apophyses; *B*, endosternite or sternal apophyses; *C*, pleural ridge; *D*, knob on the sternocostal pits of the sternum that supports the endosternite; *E*, inner curved pleural edge of the prothorax; *F*, distal end of the endosternite.

Fig. 14. The sternal apophyses of the mesothorax. *A*, arm of the endosternite; *B*, sternocostal ridge—its fixed ends; *C*, furca; *D*, inner triangular ridge of pleural suture; *E*, median prolongation of the furca.

Fig. 15. The sternal apophyses of the metathorax. *A*, anterior end of the endosternite; *B*, membrane; *C*, reduced furca; *D*, middle region of the endosternite; *E*, posterior end of the sternocostal pit.

(Fig. 19 *F*), enclosing between them the proximal end of the tibia which rests upon a flat area (*E*) on the posterior surface of the femur when the leg is extended.

The tibia (Fig. 20 *K*) is triangular and concave distally. Its proximal end bears three knobs of which one is anterior and two posterior (Fig. 17). These knobs move in corresponding grooves at the distal end of the femur, which gives them a ball-and-socket motion. The distal concavity of the tibia is more or less elliptical (Fig. 20 *H*). The posterior margin of the tibia is rounded and is prolonged (Fig. 18 *J*) beyond this elliptical area. The border of the ellipse bears long and stout bristles (Fig. 18 *B*). A thin membrane partly covers the ellipse leaving a small space posteriorly. The margin of this space is lightly sclerotized and terminates posteriorly in two diverging points (Fig. 18 *E*). These points move in the groove of the first segment of the tarsus. During the flexion of the legs a condyle (*D*) of the tarsus occupies the space (*J*) of the tibia and the tarsal region is (*I*) thrown out.

The tarsus consists of three segments ending in a pair of claws. The anterior part of the segments is thickly sclerotized, the sides thinly sclerotized, and the posterior part is covered by a very thin membrane bearing numerous minute spines (Fig. 20 *D*). Distally the first segment bears a small socket (Fig. 19 *D*) which receives the proximal end of the second tarsal segment (*C*). The second tarsal segment carries distally a socket (*B*) which receives the proximal end of the third segment. The third segment bears distally two curved hooks, and between these hooks there is a membranous area (*A*) which is very small in this segment. When the legs are deflexed, the tibia rests upon the femur, and the tarsus (except for the last segment) rests on the ellipsoid area at the distal end of the tibia.

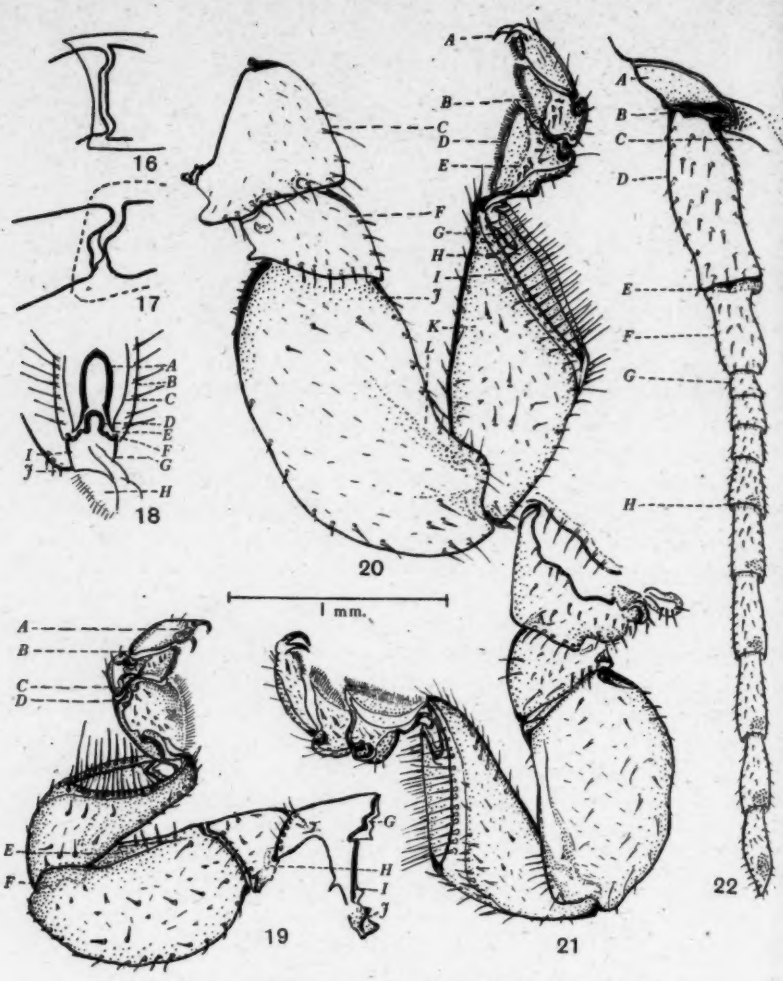
Abdomen

The terga of the abdomen (Figs. 1, 2, 3, 23–29) overlap the sterna dorsally and laterally. In the female there are nine apparent terga, and six apparent sterna (Figs. 1, 2), while the male shows eleven terga and eight sterna. The posterior margins of all the terga and sterna bear each a row of setae with a gap in the middle region.

Terga in female. The first tergum is small, and the four succeeding terga are equal in size, slightly concave posteriorly and rounded laterally. The eighth tergum has a semicircular posterior margin which has fused with the epiproct or the tail piece. The epiproct (Fig. 1 *N*) is membranous anteriorly, thinly sclerotized posteriorly, and is continuous with the single lobe of the paraproct (Fig. 3 *O*) ventrally. The fused epi- and paraproct form the telson (Figs. 1–3 *P*).

Lying below, and covered by the seventh tergum, are two thinly sclerotized sclerites—the reduced eighth and ninth terga. Taking into account these reduced terga, the apparent eighth tergum would be the actual tenth tergum and the epiproct would be the eleventh tergum.

Terga in male (Fig. 2). The end of the abdomen of many males curves



Figs. 16–22. The antenna and the thoracic appendages of *Hemimerus* (all except Figs. 16–18 are drawn to scale).

Fig. 16. Articulation of the trochanter with the femur.

Fig. 17. Articulation of the femur with tibia.

Fig. 18. Articulation of the tibia with the tarsus. *A*, space on the distal end of the tibia; *B*, bristles on the distal end of the tibia; *C*, lower part of the elliptical area; *D*, knob at the proximal end of the tarsus; *E*, chitinized pointed ends of the ellipse; *F*, proximo-lateral groove on the first tarsal joint; *G*, first tarsal segment; *H*, lower membranous area of the first tarsal joint; *I*, lower end of the proximal region of the tarsus; *J*, posterior end of the distal part of the tibia.

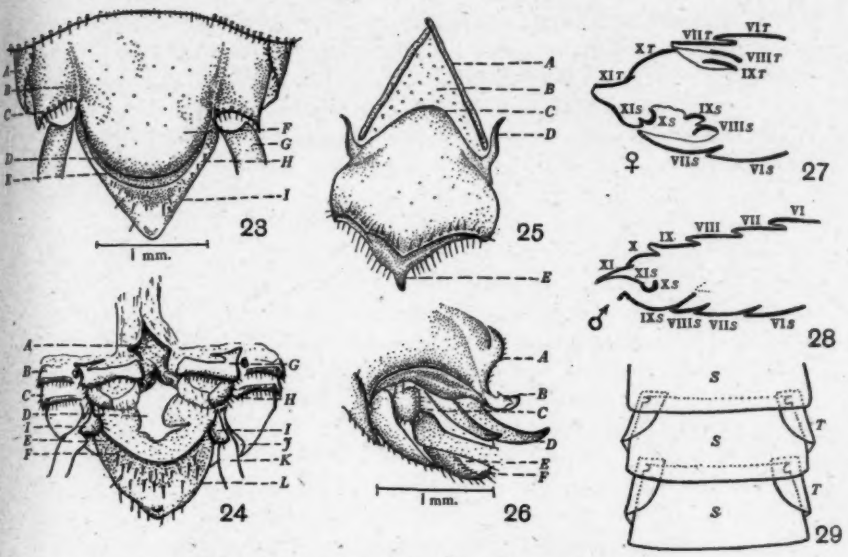
Fig. 19. The first thoracic appendage of *Hemimerus*. *A*, membranous area of the 3rd tarsal joint; *B*, *D*, sockets on the distal ends of the 1st and 2nd tarsal joints; *C*, ball-like antero-proximal end of the 2nd tarsal joint; *E*, space on the posterior surface of the femur; *F*, lateral flaps of the femur; *G*, groove on the coxa for the articulation of trochantin; *H*, sense-spots seen by Hansen; *I*, basicosta; *J*, meron.

Fig. 20. The third thoracic appendage. *A*, claws on the tarsus; *B*, *E*, 1st and 2nd tarsal joints; *C*, coxa; *D*, membranous pad on the 1st tarsal joint; *F*, trochanter; *G*, space on the distal end of the tibia not covered by the membrane; *H*, elliptical space on the distal end of the tibia; *I*, stout bristles at the distal end; *J*, femur; *K*, tibia; *L*, space on the posterior surface of the femur.

Fig. 21. The second thoracic appendage.

Fig. 22. Antenna, of the left side. *A*, antennal suture; *B*, antennifer; *C*, depression on the ventral side of the head that conceals the antenna in repose; *D*, scape; *E*, antennifer-like structure on the scape; *F*, pedicel; *G*, flagellum; *H*, sense pits.

slightly towards the ventral side. The tenth tergum has fused with the eleventh, the latter being the epiproct. The parameres (Fig. 2 *Q*) extend beyond the epiproct and are thus partly visible from the dorsal side.



Figs. 23–29. Showing the modified sterna of the male and female *Hemimerus*; and their inter-relations.

Fig. 23. The terminal region of the female exhibiting the modified 6th sternum (drawn to scale). *A*, lateral prolongation of the posterior border of the 6th tergum; *B*, proximo-lateral sulciform groove; *C*, sides of the sternum; *D*, sulciform submarginal depression; *E*, carina; *F*, conical prolongation of the 6th sternum; *G*, cerci; *H*, paraproct; *I*, telson.

Fig. 24. The aborted sterna of the female seen after removing the 6th sternum (diagrammatic). *A*, vaginal opening; *B*, *C*, reduced 8th and the 9th terga; *D*, anal cavity; *E*, line marking the border of the paraproct; *F*, paraproct; *G*, aborted 8th sternum; *H*, aborted 9th sternum; *I*, reduced 10th sternum; *J*, 7th sternum; *K*, cercus; *L*, telson.

Fig. 25. The hypandrium or the modified 8th sternum of the male (diagrammatic). *A*, rods; *B*, membrane between the rods; *C*, anterior cone of the sternum; *D*, anterior lateral processes or "Horns"; *E*, distal drawn out flat process.

Fig. 26. Terminal part of the male abdomen seen laterally (drawn to scale). *A*, conical part of the sternum; *B*, drawn out flat process of the last sternum; *C*, reduced 10th sternum; *D*, paramere; *E*, paraproct; *F*, epiproct.

Figs. 27, 28. Diagrammatic representation of the dispositions of the terminal abdominal segments of a female and a male specimen, respectively.

Fig. 29. Showing diagrammatically the postero-lateral prolongations of the terga of *Hemimerus*. *S*, sternum; *T*, tergum.

Sterna in female (Figs. 3, 29). The first abdominal sternum is absent (Imms, 1936), and the apparent first is the actual second segment. This and the succeeding sterna are covered by the lateral downward prolongations of the posterior border of the corresponding terga (Fig. 29). The apparent sixth, or

actual seventh, sternum is modified. The median part of its posterior border is semicircular (Fig. 23), and bears laterally a row of setae which overhang the bases of the cerci. From the junction of the base of the semicircle and the sides (*C*) runs a shallow groove—the proximolateral sulciform groove (Fig. 23 *B*) (Rehn). The margin of the semicircle ends in a submarginal carina (Fig. 23 *E*). Anterior to this lies a submarginal depression (Fig. 23 *D*). A thin membrane runs below this segment to the reduced eighth and ninth sterna (Fig. 24 *G, H*) which are at the sides of the opening of the vagina and the anus. At the sides of these reduced sterna are situated the reduced terga (*B, C*). At the base of the cerci lies the reduced tenth sternum (Fig. 24 *I*). It is small and semicircular on the inner side and bears a row of bristles. The paraproct is the eleventh sternum.

Sterna in males (Figs. 25, 26). The second, third and fourth sterna are nearly alike. The fifth, sixth and seventh, gradually decrease in size and have each a concave posterior border. The apparent eighth sternum is highly modified (Fig. 25). The posterior border is drawn out into a flat process which has a sclerotized margin, and is inclined towards the right side. The body of sternum is convex dorsally. The anterior part lies covered by the sixth and seventh sterna, and is drawn out into a cone (Fig. 25 *C*). The sides of the cone are drawn out into curved pointed horns (Fig. 25 *D*). On each side at the bases of these horns lies a sclerotized rod (Fig. 25 *A*) which meets its fellow of the opposite side and encloses a membrane (*B*).

This complex sternum covers the anal and the genital opening and Crampton (1918) had coined the word hypandrium for such segments. Inside this hypandrium, and covering the bases of the cerci at the sides, lies the aborted tenth sternum.

The homology of the rods is doubtful. I believe they act as levers in throwing out the male genital apparatus and also in bending the distal end of the abdomen. The great development of muscles in this region, and their connexion with the copulatory apparatus, tend to confirm this view.

Cerci. Unsegmented cerci covered by thin hairs and setae are present in both male and female. They are not equal in size, and the curving of the tip is more evident in the male.

Summary

The present work, fills in some of the gaps in the morphological descriptions of *Hemimerus*, as given by Hansen (1894) and Jordan (1909), and deals with the details of the anatomical modifications associated with the semiparasitic mode of life.

It seems that this semiparasitic mode of life is of mutual assistance or "symbiosis".

The modifications are seen in the mouthparts (especially the ligula and the superlingua), pleural sclerites and the thoracic limbs.

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SOME MICROSPORIDIA FOUND IN CERTAIN FISHES AND INSECTS IN EASTERN CANADA

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(With Plate V, containing Figs. 1–74, and 1 Figure in the Text)

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Introduction

Eastern Canada, with its numerous lakes, rivers and streams, affords not only an enormous field for animal ecology, but also a largely untouched field for investigations of its animal parasites. In this connexion, we have been able to observe a relatively large number of new species of Neosporidia. Two papers on Myxosporidia have already appeared (1939, 1940), and the present paper is a contribution to knowledge of some new and some already recorded Microsporidia of certain fishes and insects. While a number of other species of

Microsporidia have been under observation, description of them is deferred until fuller investigations have been made.

MATERIAL AND METHODS

The fresh-water fishes were obtained from sites in Quebec Province, the topography of which was recently described by us (1939). The marine fishes were freshly caught and examined in Halifax, Nova Scotia and St Andrews, New Brunswick. Also, some fish were bought at local fish shops in Montreal, the infections obviously being very slight and unrecognizable to the untrained observer. The aquatic insects were collected as larvae or nymphs from ponds and small streams in the vicinity of Montreal or Quebec City. Infected hive-bees and humble-bees were obtained from various places near Quebec City and Montreal.

Fresh preparations in normal saline solution, with or without neutral red, methyl green or methylene blue as intra-vitam stains, were always used. Stained smears and sections were made as far as the amount of material permitted, haematein, Heidenhain's iron haematoxylin and Giemsa stains being employed. Some useful results were obtained from preparations that were first much overstained and then gradually destained. A dark-ground condenser was useful. All drawings were made with a camera lucida.

THE MICROSPORIDIA OBSERVED

Regarding classification, we have chiefly followed that of Léger & Hesse (1922), as modified by Kudo (1924), which also has been mainly used in Doflein (1929) and Reichenow (1932). The Microsporidia we have examined belong to the suborder Monocnidea Léger & Hesse (1922), family Nosematidae Labbé, 1899. Kudo includes the genera *Nosema*, *Glugea*, *Perezia*, *Gurleya*, *Thelohania*, *Stempellia*, *Duboscqia* and *Plistophora* in the Nosematidae. In Doflein's *Lehrbuch* (1929), *Perezia* is placed as a synonym of *Glugea*, but, in view of its morphology and simpler mode of development and also the contradictory accounts and views regarding *Glugea*, we have preferred to retain the genus *Perezia*. Some workers also put *Glugea* in a separate family, the Glugeidae.

The Microsporidia herein described or notified are:

Nosema pimephales n.sp. from *Pimephales promelas*.
Nosema branchiale Nemeczek, from *Gadus callarias*.
Nosema apis Zander, from *Apis mellifica*.
Nosema bombi Fantham & Porter, from *Bombus vagans*.
Glugea hertwigi n.var. *canadensis*, from *Osmerus mordax*.
Glugea stephani Woodcock, from *Pseudopleuronectes americanus*.
Perezia aeschnae n.sp., from *Aeschna grandis*.
Perezia legeri Paillot, from *Pieris brassicae*.

Gurleya aeschnae n.sp., from *Aeschna grandis*.

Thelohania corethrae Schuberg & Rodriguez, from *Chaoborus flavicans*.

Thelohania bracteata (Strickland) Debaisieux & Gastaldi, from *Simulium bracteatum* and *S. venustum*.

Thelohania fibrata (Strickland) Debaisieux & Gastaldi, from *Simulium venustum*.

Nosema pimephales n.sp.

(Pl. V, figs. 1–18)

An interesting *Nosema*, apparently new to science, has been observed by us in one young *Pimephales promelas* out of a number collected from Lake Guindon, Province of Quebec. Heavy infections, which may be due to this *Nosema*, have been reported among young *Pimephales* in this district, fish 12–15 mm. long being chiefly affected.

The infected fish had a large cyst which greatly distended the abdomen and practically obliterated the coelomic cavity. The intestine was much compressed by the tumour and its lumen considerably reduced. The pancreatic tissue also was reduced. All the veins of the abdominal viscera were congested. The wall of the cyst or tumour consisted of fibrous reaction tissue, surrounding a mass of multiplicative stages and spores of a *Nosema*.

Morphology

Some details of the morphology of this *Nosema* may now be given.

The planont or amoebula stage. The planont or amoebula stage is a very small body up to 2μ in diameter and is either uninucleate or binucleate. Very few amoebulae have been observed.

Schizogony or merogony. The young trophozoites or meronts vary in size, the smallest being about 1·5–2·2μ in diameter, but many measured about 3 by 2·6μ in diameter. The cytoplasm of such forms is finely granular and homogeneous (Fig. 1). The nucleus is sometimes karyosomatic but, prior to division, contains several large chromatin granules which vary in number.

Schizonts are fairly numerous. Some divide into two, the nucleus dividing first, the daughter forms remaining attached by cytoplasmic strands at first but eventually separating. Others divide into two so far as the nucleus is concerned, but there is no immediate cytoplasmic cleavage (Figs. 2, 3), though these ultimately separate into two. Such dividing forms are also shown in Figs. 4, 5. Yet other schizonts undergo repeated nuclear multiplication, parasites with four, six (Fig. 8) and more nuclei being observed, these ultimately breaking up into uninucleate portions. Clusters of meronts (Figs. 6, 7) have been found in some parts of the cyst, some of the components having formed individual units while others are in the form of dumb-bells, their cytoplasmic strands not having parted

Sporogony. Sporogony is the dominant stage in the cyst. One sporoblast, which is formed by each uninucleate meront, gives rise to one spore, which is characteristic of the genus *Nosema*. In the young sporoblast and spore, a vacuole appears at one pole and often the nucleus is to be seen at the opposite pole (Figs. 9, 10). The cytoplasm appears to contract and become girdle-like (Figs. 11–13), the nuclei passing towards the centre. Nuclear multiplication occurs, a polar filament gradually differentiates within the polar capsule, and a complete young oval or elliptical spore finally contains two sporoplasmic nuclei, one capsulogenous nucleus and one or very occasionally more sporocyst, valvular or parietal nuclei. As we have observed in *N. apis* (1912), *N. bombi* (1914), *N. cactoblastis* and *N. cactorum* (1938), progressive degeneration of the capsulogenous and parietal nuclei occurs, the parietal nucleus (Fig. 10) being generally the first to disappear. They are usually small, compact, elongate chromatin bodies. The capsulogenous nucleus at first is karyosomatic and nearly the size of the sporoplasmic nuclei, but rapidly becomes a smaller, homogeneous mass (Fig. 11). The sporoplasmic nuclei are small, rounded and karyosomatic, with occasionally extra-karyosomatic chromatin granules (Figs. 11, 17). The nuclear membrane is practically uniform in thickness. The spore-wall is smooth. The polar filament is usually coiled within the polar capsule (Figs. 13–17). Fully extruded polar filaments have been but rarely observed (Fig. 18), but the few found measured 70–90μ in length. Usually small portions only of the filament have been extruded on pressure.

The majority of the spores vary in length from 3·8 to 4·4μ, but very rarely a spore reaching 5·2μ in length has been observed. The breadths of the spores vary from 1·9 to 3·3μ, the latter breadth being exceptional.

Systematic position

As one sporoblast produces one spore, this microsporidian is a member of the genus *Nosema*.

There appears to be but few species of *Nosema* recorded as parasites of fishes. Lutz & Splendore (1903) briefly notified *N. girardinus* from the skin, muscles, serosa and intestinal mucosa of *Girardinus caudimaculatus*. Its spores were pyriform, 2–2·5 by 1–1·5μ, these dimensions being much smaller than those of the spores of the *Nosema* of *Pimephales*. Doflein (1898) described a *Glugea* from the nervous system of *Lophius piscatorius*, this being transferred to the genus *Nosema* by Pace (1908), a procedure also adopted by Weissenberg (1911). Doflein described the spore as being often curved. Weissenberg found two types of spores, one cylindrical, the other oval. Doflein's spores were 3·5 by 1·5μ in diameter and so, like those of *N. girardinus*, are much smaller than those of the *Nosema* of *Pimephales*. *Glugea punctifera* was described by Thélohan in 1895. It was parasitic in the connective tissue of the eye muscle of *Gadus pollachius*. The spore was ovoid, 4–5 by 3μ. Labbé, in his work on Sporozoa

(1899), transferred *Glugea punctifera* to the genus *Nosema* as *N. punctifera*, but Kudo (1924) reclassified it as *Glugea punctifera*. Labbé also placed *G. acuta* Thélohan, parasitic in the fin muscles of *Syngnathus acus* and *Nerophis aequorum*, in the genus *Nosema*, but Kudo (1924) accepted Thélohan's classification. Owing to the paucity of details in the original descriptions, it would seem best to adopt the original classification of Thélohan. So far as the *Nosema* of *Pimephales* is concerned, it cannot be assimilated with either of the forms considered by Labbé to be parasitic in fishes. *Nosema branchiale*, described by Nemeczek (1911) as a parasite of *Gadus aeglifinis*, is regarded by Kudo (1924) as doubtfully belonging to the genus *Nosema*. However, herein we give some additional information regarding a *Nosema* which we consider to be *N. branchiale*, parasitic in *Gadus callarias*, the spores of which are larger than those of the parasite of *Pimephales*. As far as we can ascertain, these are all the species of *Nosema* recorded from fishes, nor do there appear to be any from other vertebrates with which it can be assimilated. Species of *Glugea* and *Plistophora* are much more common than *Nosema* in vertebrates.

The possibility of the *Nosema* infection of *Pimephales promelas* having been acquired from some invertebrate with a common habitat has been considered. In Canada this reduces to infection from some aquatic insect larva or crustacean with which the fish might come in contact or on which it might feed. We know of one species of *Nosema* (as yet undescribed) in an Ephemerid larva and another undescribed one in a Trichopteran larva, but both have spores much smaller than those of the *Nosema* of the fish. *N. schneideri* Léger & Hesse (1910) is parasitic in larvae of *Ephemera vulgata* in France. Its spores are 4 by 2μ and its polar filament 90μ long. We have not found *Nosema schneideri* in Canadian Ephemerids. The infection of larval and adult *Anopheles quadrimaculatus* and *Anopheles* sp. in Georgia, U.S.A., with *Nosema anophelis* has been described by Kudo (1924). Fresh spores measured 4·7–5·8 by 2·3–3·2μ, stained ones varying slightly with different hosts, the range being 4–4·5 by 2–2·5μ. The spore membrane is weak, and slight pressure causes the extrusion of the polar filament which is 50–60μ long. The spore of *N. anophelis*, thus, is very unlike that of the *Nosema* of *Pimephales*. Also, the numerous larvae of *Anopheles* examined by us have not shown any infected with *Nosema anophelis*. We have not found the fish parasite in various Cladocera and Copepoda examined. The source of infection of the fish is obscure and the *Nosema* does not agree morphologically or in spore dimensions with species recorded from aquatic insects or Crustacea from which it could have acquired infection. It would appear, then, that the *Nosema* from *Pimephales promelas* from Quebec Province, Canada, is a new species, occurring in a new host and in a new locality. It is, therefore, designated *Nosema pimephales* n.sp., with characters as herein described.

Nosema branchiale Nemeczek

(Pl. V, figs. 19–28)

A microsporidian, which we think is probably *Nosema branchiale* Nemeczek, has been found in a minute, whitish cyst, about 1 mm. diameter, on a gill filament of a cod, *Gadus callarias*, bought in Montreal but stated to have been caught off the Gaspé Coast. On attempting to remove the cyst, it ruptured and a milky fluid came out. Smears were made and fresh preparations in normal saline solution examined, with and without vital staining. Much debris and epithelium were present, together with schizonts and a few spores of a *Nosema*. The cyst wall was composed of fibrous reaction tissue.

Schizogony. The youngest forms observed are rounded to triangular bodies (Fig. 19) with granular cytoplasm and a small nucleus. These increase in size and multiply by binary fission (Fig. 20). This may be repeated with or without complete separation of the meronts. Sometimes clusters of meronts have been seen (Figs. 21, 22), resulting from division in more than one direction. At other times, division is in one direction only, resulting in the production of chains (Fig. 23), similar to those often produced by *N. apis* and *N. bombi*. Ultimately the meronts separate and sporogony follows.

Sporogony. Each meront at the end of its growth develops into one sporoblast which forms one spore. Sporoblasts with two round, adjacent, karyosomatic nuclei have been seen, and others in which further nuclear multiplication has occurred and the beginnings of a polar capsule with its capsulogenous nucleus are present (Fig. 24). Spores (Figs. 25–28) are more or less elliptical in outline. They measure 5·7–6·6 by 3·5–4·2μ, most of those measured being 3·5–3·8μ in breadth. The spore wall is thin and smooth. The parietal nuclei are at first oval (Fig. 24) but become linear (Fig. 26) and finally disappear. The sporoplasm is very granular. The sporoplasmic nuclei are relatively large, with distinct karyosomes (Figs. 26, 27). The polar capsule and vacuole are well defined. In a few spores some coils of the polar filament have been demonstrated by vital staining (Fig. 27). Under considerable pressure a few spores ejected their polar filaments, which measured 75–90μ in length. One such spore is shown in outline in Fig. 28.

Systematic position

Since one sporoblast gives rise to a single spore, this microsporidian from *Gadus callarias* belongs to the genus *Nosema*. Nemeczek (1911) briefly described the "cyst" and spore of a *Nosema* from *Gadus* (=*Melanogrammus*) *aeglifinis* in Austria. The multiplicative stages were not described but the spores were 6·3 by 3·5μ, oval and with a large vacuole, judging from the illustration of the parasite, this being a spore with the polar filament extruded. The polar filament reached 90μ in length. The "cyst" was compared by Nemeczek with

that of *Glugea anomala*. The incomplete account caused Kudo (1924) to remark on its systematic position thus: "Nemeczek's observations on the vegetative form are inadequate to assign this form definitely to this genus [*Nosema*]. Since he compares the 'cyst' with that of *Glugea anomala*, he may have had a species of *Glugea* although he designated it as a *Nosema*." This statement was justified by the original description. However, we think that we have probably been dealing with the same organism as Nemeczek. Unfortunately, there are only features of the spore for comparison. The dimensions of the spores of the Canadian *Nosema* are 5·7–6·6 by 3·5–4·2μ. *N. branchiale* has spores 6·5 by 3·5μ, that is, within our range. The polar filament of the Canadian *Nosema* has reached 90μ long, that of *N. branchiale* 100μ. The differences, then, are very slight. We have been fortunate in finding some of the schizogonic stages which establish the parasite as a species of *Nosema*. The host of the Austrian *N. branchiale* is *Melanogrammus aeglifinis*, that of the Canadian *Nosema* is *Gadus callarias*, both hosts belonging to the family Gadidae. For the present, therefore, the Canadian *Nosema* is considered probably to be the same as *N. branchiale* Nemeczek and is so designated.

Nosema apis Zander

Nosema apis has been observed as slight infections of the alimentary tracts of hive-bees caught in the vicinity of Montreal. The infected bees were few in number but were crawling on the ground. Spores of *N. apis* were recovered from adjacent vegetation. *N. apis* in Canadian bees has the same morphology as we described for European bees (1912, 1912*a*,*b*) and it and a *Gregarina* previously noted by us were the only Entozoa observed. One bee mite, *Braula caeca*, was attached to one bee. *Acarapis* (=*Tarsonemus*) *woodi*, parasitic in the tracheae of bees, was sought for but not found either in normal hive-bees or in those infected with *Nosema apis*.

Nosema bombi Fantham & Porter

Nosema bombi Fantham & Porter (1914) has been observed in the malpighian tubes of a few specimens of the nest-building humble-bee, *Bombus vagans*, caught near Lantier, Province of Quebec. Its morphology was in no way different from that of *Nosema bombi* as observed by us in various species of *Bombus* in England, but we found no evidence of epizootics among *B. vagans*. The distribution of *Nosema bombi* is extended to Canada.

Glugea hertwigi n.var. **canadensis**

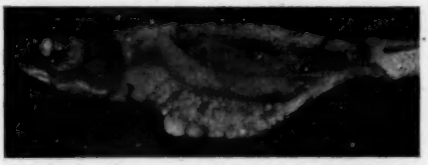
(Pl. V, figs. 29–42, and Text-fig. 1)

Among a number of smelt, *Osmerus mordax*, collected by one of us (L. R. R.) from Lake Edward, one contained small cysts situated in the serous membrane of the hindgut. The cysts are extremely thin-walled, but are surrounded by a

fairly thick zone of mostly fibrous connective tissue, this being reaction tissue produced by the host. The cysts formed aggregations in some parts (see Text-fig. 1), as many as seven cysts in contact with each other lying between the two surfaces of the serous coat. Occlusion of lymph spaces and some leucocytic infiltration with pus formation were present. The cysts contained a parasite which appears to be a distinct variety of *Glugea hertwigi* Weissenberg (1911, 1913).

Morphology

The amoebula or planont. The young amoebula or planont, freshly issued from the spore, is a small organism, many of those observed being about 1–1·5μ in diameter. Usually they are roughly rounded or oval; very occasionally a small, blunt pseudopodium has been observed. Larger ones (Pl. V, fig. 29) have finely alveolar cytoplasm and a nucleus, often with an excentric karyosome. The amoebula by growth becomes the schizont.



Text-fig. 1. *Osmerus mordax* showing cysts of *Glugea hertwigi* var. *canadensis*. Untouched photograph. L.R.R.

Schizogony. The young amoebula, having invaded the serosa, apparently settles down and becomes the schizont, forming finally a plasmodial mass. Examination of young cysts shows that there is a peripheral zone of cytoplasm containing numerous nuclei. Beyond this zone is a number of small rounded nuclei in groups surrounded by cytoplasm and these gradually are replaced by rounded to oval forms each with a differentiated cell membrane, usually with homogeneous but occasionally vacuolated cytoplasm and a rounded, karyosomatic nucleus. These are often about 2·3–3·3μ in diameter. With these are more elongate, that is, tubular forms (the cylinders of Weissenberg), which are thin-walled, containing alveolar cytoplasm and sometimes one but usually two relatively large nuclei. Such bodies usually range from 3 to 5·4μ in length and from 2 to 3μ in breadth. Gradually the alveolar cytoplasm differentiates into two distinct masses, one around each nucleus. The nuclei are usually homogeneous in structure; in a few cases only has a distinct karyosome been observed. These binucleate tubular forms are from 4·6 to 7·7μ in length and from 1·5 to 3·5μ in breadth. In some of these, growth accompanied by further nuclear division occurs (Figs. 30, 31), which, being repeated, results in larger multinucleate masses, containing eight or more nuclei (Figs. 32, 33). In some of these, further divisions were incipient. Usually forms with eight or sixteen

nuclei were observed. These resemble the elongate schizonts found in such forms as *Nosema apis* and other Microsporidia, as Weissenberg (1913) has noted.

Sporogony. At the onset of sporogony, segregation of cytoplasm around nuclei or incipient nuclei of the larger tubular schizonts has been observed (Figs. 33, 34). The formation of uninucleate sporoblasts from the schizont may be simultaneous or occur in irregular series. Fig. 34 shows two recently divided schizonts, each of which will ultimately form four uninucleate sporoblasts. After growth, the nucleus of each uninucleate sporoblast divides into two, and the cytoplasm gradually becomes alveolar as spore walls are produced. Segregation of the cytoplasm into two portions occurs (Fig. 37) and ultimately two spores are produced.

The spores are elongate-ovoid to somewhat sausage-shaped bodies (Figs. 38–42). They are not easily stained to show internal structures sharply, but the following features have been observed in smears and sections. There is a cytoplasmic mass often bordering the periphery of two-thirds of the spore and continuous with a band-like mass across the short axis of the spore (Figs. 38–42). A cavity corresponding to the polar capsule is present (Figs. 38–41), and within this, in some specimens, coils of the polar filament could be observed. Sometimes they appear to be across the entire width of the spore (Figs. 38, 39), in other spores they are restricted to a lateral area (Figs. 41, 42). The two sporoplasmic nuclei are small, rounded, karyosomatic bodies sometimes arranged tandem (Figs. 38, 41, 42), sometimes transversely across the spore (Figs. 39, 40). In some cases nuclear separation has been incomplete, a chromatin thread uniting the two, while in others one nucleus only has been seen. These nuclei are not easily differentiated. The spores are 3·5–4·6μ in length and 1·5–2·3μ in breadth.

Systematic position

A *Glugea* has already been described by Weissenberg (1911, 1913) from the European smelt, *Osmerus eperlanus*, as *Glugea hertwigi*, its spores being 4·5–5·4 by 2·3μ. Linton (1901) recorded a *Glugea* from smelt in the United States, and Schrader (1921) notified *G. hertwigi* from the smelt, *Osmerus mordax*, from fresh and salt water in the United States, its spores being 4–4·5 by 2–2·3μ. Schrader considered that the parasite was *Glugea hertwigi* and specific for smelt. Mavor (1915) mentions that he had seen *Osmerus mordax* infected with a microsporidian, which he considered to be *Glugea stephani*. If this were the same form as was observed by Schrader in the same host, the dimensions do not seem to fit with this diagnosis or with what we think is *G. stephani* observed by us in flat fish in Canada. The *Glugea* we have had under observation in Canadian *Osmerus mordax* agrees in general morphology and development with *Glugea hertwigi*, but the situation and disposition of the polar filament are rather different. The range of dimensions of the spores is 3·5–4·6

by 1·5–2·3μ, the smallest lengths and breadths being less than those recorded by previous workers on *G. hertwigi* from smelts. However, Bond (1938) has described briefly cysts and spores of a *Glugea* that he considers to be *G. hertwigi* from *Fundulus heteroclitus* from Maryland, U.S.A. In sections the spores were 3–4 by 1–1·5μ, which is much smaller than our form. For the present, it seems advisable to classify the *Glugea* of Canadian *Osmerus mordax* with that of the European smelt, *O. eperlanus*, and *O. mordax* of the United States, but on account of the differences previously mentioned, the Canadian form appears to be a distinct variety, for which the name *Glugea hertwigi* var. *canadensis* is suggested.

Glugea stephani (Hagenmuller) Woodcock

A *Glugea* has been observed in *Pseudopleuronectes americanus* and *Limanda ferruginea*, the fish having been caught off the coast near Halifax and sent entire to us by a friend; consequently, they were not quite fresh when received in Montreal. Cysts were present in the submucosa of the intestine, the general description of which corresponded with those of *Glugea stephani*. The descriptions of *G. stephani*, unfortunately, are inadequate for exact determination, and also our material was not quite fresh. The cysts from *Pseudopleuronectes americanus* and from *Limanda ferruginea* were identical in structure and contents. The former has already been reported as a host of *Glugea stephani*, but *Limanda ferruginea* seems to be a new host.

Perezia aeschnae n.sp.

(Pl. V, figs. 43–52)

When examining a collection of nymphs of the large dragon-fly, *Aeschna grandis*, from the neighbourhood of Montreal, we have been able to make some observations on a large species of the microsporidian, *Perezia*. One nymph out of forty-one harboured a slight infection in a few of the cells of its fat body. The infected cells had a chalky white appearance but were not noticeably hypertrophied.

Morphology

The young trophic forms observed are more or less rounded bodies with granular cytoplasm. All those observed had two crescentic to bean-shaped nuclei adjacent to each other (Fig. 43). These trophic forms give rise to schizonts.

Schizogony. The schizonts at first are binucleate and rounded. They grow, and nuclear multiplication occurs, rounded forms with two groups of two nuclei and dense staining cytoplasm being produced (Fig. 44). Such rounded schizonts are 4·4–6·9 by 4·1–5·5μ. The nuclear division can be repeated and the binucleate daughter forms remain attached to one another without cytoplasmic

cleavage for some time (Fig. 45). Such chains of schizonts range in length from 16 to 20·7μ and in breadth from 2·2 to 4·1μ. There are considerable differences both in the size and appearance of these chains. Ultimately the individuals separate and sporogony ensues after a period of growth and elongation of the individuals.

Sporogony. At sporogony the cytoplasm of the meronts loses its deep-staining properties and vacuoles appear. Nuclear division into two sets of two nuclei occurs, and the daughter nuclei migrate in pairs towards the ends of the sporoblast, which becomes somewhat halter-shaped (Fig. 49). The concentration of nuclei and cytoplasm continues and ultimately an ovoid spore is produced at each end (Fig. 50). Each spore (Figs. 51, 52) has two crescentic to oval-shaped nuclei and is difficult to stain. A vacuole or polar capsule differentiates at the broader end and very occasionally indications of a polar filament can be made out. On very few occasions the ejection of polar filaments under pressure has been observed (Figs. 51, 52), such measuring up to 80μ in length. The spores are large, varying from 5·9 to 7·4μ in length and 3·3 to 4·6μ in breadth.

Systematic position

The number of species of *Perezia* hitherto recorded does not seem to be large. The type species, *Perezia lankesteriae* Léger & Duboscq (1909), is parasitic in the gregarine, *Lankesteria ascidiae*. Three species are parasites of larvae of *Pieris brassicae*. *Perezia mesnili* Paillot (1918) is parasitic in the malpighian tubules; *P. legeri* Paillot (1918*a*) is a parasite of the fatty tissue and giant cells of the blood, and *P. pieris* Paillot (1924) occurs in the malpighian tubules and the silk glands. *Perezia pyrausta* Paillot (1927) infests the malpighian tubules and silk glands of the caterpillar of *Pyrausta nubilabis*. Our species of *Perezia* is parasitic in cells of the fat body of the nymph of the dragon-fly, *Aeschna grandis*, thus extending the distribution of the genus *Perezia* in Insecta to the Odonata. The schizogonic stages of the dragon-fly *Perezia* are nearer in structure to those of *P. mesnili* and *P. legeri*. The size of the spores, 5·9–7·4 by 3·3–4·6μ, is greater than that of *P. mesnili* (3·4 by 1·5–2μ), *P. legeri* (4–5μ long), *P. pieris* (as calculated from Paillot's drawings) and *P. pyrausta* (4·7–5·9 by 2–2·6μ). From the foregoing, it appears to be a distinct species, occurring in a new host and a new locality and is, therefore, designated *P. aeschnae* n.sp., with characters as herein set forth.

Perezia legeri Paillot

A species of *Perezia*, which we consider to be *P. legeri* Paillot (1918), has been found in small numbers in cells of the fat body in two out of thirty-seven larvae of *Pieris brassicae* collected near St Martin, a few miles from Montreal. This appears to be the first record of *Perezia legeri* for the North American continent.

Gurleya aeschnae n.sp.

(Pl. V, figs. 53–59)

A new species of *Gurleya* has been found parasitic in cells, probably oenocytes, at the surface of the fat body of one out of forty-one nymphs of the large dragon fly, *Aeschna grandis*. The infection was slight, the host cells being denser and whiter than normal cells. Sporogonic stages predominated.

Schizogony. The trophozoites about to become schizonts are roughly rounded bodies. Their cytoplasm is granular and fairly homogeneous. At first, each is uninucleate, with a relatively large nucleus, large karyosome and some chromatin granules on the nuclear membrane. At the onset of schizogony the chromatin segregates into two masses at either pole of the nucleus and division by binary fission occurs. The cytoplasm elongates, a nucleus migrates to either end and a tubular schizont is formed (Fig. 53). Most of such binucleate schizonts are about 11μ long by 3·4–4·1μ wide. The division appears to be repeated several times, and ultimately the daughter forms separate from the schizont as rounded bodies, which grow rapidly and become the pansporoblasts or sporonts.

Sporogony. The pansporoblasts are rounded bodies from 10·7–11·8 by 8·3–10·4μ. At the onset of sporogony the nuclear chromatin forms a series of granules (Fig. 54), which reconstitute themselves into two nuclei, each with a karyosome and granules of chromatin on the nuclear membranes (Fig. 55). Their cytoplasm is pale staining. A second division produces the tetranucleate stage (Fig. 56). Cytoplasmic segregation follows and the tetranucleate sporoblast gives rise to four spores (Figs. 57, 58). Such sporoblasts containing spores are often 12·9–14·4 by 8·5–10·4μ and are oval in outline. The remains of the pansporoblast or sporont forms a common membrane around the spores.

The spores (Fig. 59) are ovoid to pyriform, 5·5–6·6 by 3–4·1μ. At the broader end there is a vacuole-like structure, probably representing the polar capsule, adjacent to the base of which there is often a chromatoid mass that is considered to be the closely coiled polar filament. Very occasionally a dot-like mass of chromatin, the capsulogenous nucleus, has been detected. In some spores a small, rounded, karyosomatic, sporoplasmic nucleus has been demonstrated by long staining with methyl green, this nucleus often being surrounded by strands of deeply staining cytoplasm. The extrusion of the polar filament has not been observed. Differentiation of macrospores and microspores, such as Hesse has described for *Gurleya legeri*, has not been observed, but, unfortunately, our material was scanty.

Systematic position

The genus *Gurleya* was founded by Doflein in 1898 for *G. tetraspora*, parasitic in *Daphnia*, characterized by the production of four spores from one sporont or pansporoblast. Unfortunately the dimensions and magnifications for

the illustration were omitted. The spores had fine striations or ridges on their surface. *Gurleya legeri* Hesse, 1903, occurs in nymphs of *Ephemerella ignita* and has been notified from a larval caddis fly by Mackinnon (1911). Pansporoblasts developed microspores or macrospores. The pansporoblasts with microspores were 11 by 5μ, those with macrospores 5–8μ or 8 by 6μ. The macrospores were 5–6 by 3–4μ, the microspores 4–5 by 2·5μ. Polar filaments were 24–25μ long. Mackinnon did not describe macrospores and microspores, the spores found being 4–5 by 2·5–3μ. *Gurleya francottei* Léger & Duboscq, 1909, 1909*a*, occurs in the larva of *Ptychoptera contaminata*. The spores are pyriform, 3μ long, and the spores characteristically become united or attached crosswise at their rounded ends. *Gurleya richardi* Cépède, 1911, parasitic in *Diaptomus castor*, has subcircular schizonts. The pansporoblasts produce either macrospores or microspores, macrospores being 5·5–6 by 2·8μ, while microspores are 4–4·5μ long. Polar filaments are 45μ long. *Gurleya cyclopis* Leblanc, 1930, from *Cyclops albidus*, is distinguished by having its four spores in a bundle or packet without any distinct investing membrane or envelope. The spores are curved, pear-shaped and large, being 16·5μ long and 3μ broad. Its polar filament, ejected under the influence of glycerine, is 30μ long and has a spirally coiled free end.

There are, thus, relatively few previously described species of *Gurleya*. The *Gurleya* from the nymph of *Aeschna grandis* differs from the type species, *Gurleya tetraspora* Doflein, in having spores with smooth and not ridged walls. It is unlike *G. legeri* Hesse in apparently having but one type of spore, in the arrangement of the spores in the pansporoblast and in the spores being larger and much less pointed. *G. francottei* Léger & Duboscq has spores of one type, but these are much smaller and are arranged in a cruciform manner. It also differs from *G. richardi* Cépède which has macrospores and microspores, of which the general structure, appearance and range of dimensions of the spores are different. *G. cyclopis* Leblanc is easily distinguished from the *Gurleya* of *Aeschna grandis*, being so much larger, having a different arrangement of the spores which are without remains of the pansporoblast around the cluster and having globules attached to the very large spore. The *Gurleya* from the nymph of *Aeschna grandis*, then, differs from previously described species, it occurs in a new host and is the first *Gurleya* to be recorded from the Odonata. It is therefore considered to be a new species and is designated *Gurleya aeschnae* n.sp., with characters as herein set forth.

Thelohania corethrae Schuberg & Rodriguez

(Pl. V, figs. 60–74)

A species of *Thelohania* has been observed in the oenocytes of two larvae of *Chaoborus flavicans* Meigen, which, in American literature, is sometimes named *Corethra albipes*. The infected larvae were collected on two occasions from a

pond near Montreal West by Mr J. R. Adams, M.Sc., to whom our best thanks are due for this interesting material and for particulars regarding the *Chaoborus*. This pond has been under observation by Mr Adams since 1935, and the Corethrid appeared there for the first time in 1938 in the autumn, and a second infected individual was found in a collection made in November 1939. One anterior and two posterior segments of the first larva contained cysts of the parasite, and one anterior segment of the second larva contained a small cyst of the same *Thelohania*.

Morphology

The youngest stages observed have been amoebulae or planonts. These are small, oval to conical bodies, with rather dense, homogeneous cytoplasm and a single, large, karyosomatic nucleus. Most of those seen were about 2·3 by 1·5μ in diameter. Larger amoebulae are binucleate. Sometimes the nuclei are close together (Fig. 60), at other times farther apart. Very occasionally traces of pseudopodia have been seen.

Schizogony. Some uninucleate forms with the nucleus in process of division have been observed. These divide and the binucleate forms elongate and become more or less oval (Fig. 61). Their nuclei migrate towards each pole (Fig. 62) and constriction of the cytoplasm occurs, though often the daughter forms (meronts) remain attached. The nuclei divide again (Fig. 63) and tetranucleate schizonts result (Fig. 64). Another division results in four clusters of two nuclei (Fig. 65), these remaining close together. Gradual cytoplasmic constriction and another nuclear division occur, whereby rosettes of eight binucleate daughter forms are produced (Fig. 66). These finally separate. As in *Nosema*, a single meront may divide directly into two. During schizogony there is great increase in size of the growing parasites. Growth, division and separation rates are unequal, resulting in considerable morphological variation. The cytoplasm of schizogonic forms is densely staining and granular. Some extranuclear chromatin granules may be present (Fig. 62).

The dimensions of all stages in schizogony, naturally, vary. Most uninucleate forms observed were from 3·3–4·2 by 4·2–4·8μ. Some binucleate schizonts or meronts measured were 4–6·2 by 2·7–4·8μ. The tetranucleate forms varied considerably, individual small ones being 3·8 by 4·2μ and larger ones 6·2 by 3·3μ. The diameters of rosettes of binucleate meronts were often about 12·7 by 11·9μ and 13·1 by 10·2μ.

Sporogony. The binucleate individuals produced from a schizont are the starting point for sporogony. By growth they become pansporoblasts (Fig. 67). Their cytoplasm becomes much vacuolated and stains more faintly, as was noted by Schuberg & Rodriguez (1915). The two nuclei divide twice (Figs. 68, 69) and cytoplasmic fission may follow, so that two spherical masses are produced, or the daughter forms may remain attached. Division is repeated

(Fig. 70), and ultimately eight binucleate sporoblasts are produced from each pansporoblast (or sporont), the cytoplasm condensing around each group of two nuclei (Fig. 71). There is much variation in the size of the sporoblasts with eight clusters of nuclei. The cytoplasm becomes much more difficult to stain, as some of its stainable constituents are used in the formation of the valves or walls of the spores, which gradually differentiate (Fig. 72).

The spores (Figs. 73, 74) are oval in outline. A vacuole is present at one end and a polar capsule area containing a polar filament at the other. Traces of the polar filament have been seen in some stained spores (Fig. 73). Spores with partly extruded polar filaments (Fig. 74) and some with apparently completely extruded filaments, 18–38μ in length, have been observed. The sporoplasm is often girdle-like but sometimes forms a layer lining the valves, with a girdle-like central mass (Fig. 73). The sporoplasmic nuclei are small, rounded (Fig. 73) to oval (Fig. 74) bodies. Two, or occasionally one, may be present. In some spores two small, oval, granule-like parietal nuclei have been seen and very occasionally a larger, deeper-staining chromatoid granule has been found in the neighbourhood of coils of the polar filament, which may be interpreted as a capsulogenous nucleus. The various components of the spore are not easy to interpret, and their appearance varies both with the age of the spore and to some extent with the method of staining employed. The spores show a wide range of dimensions, varying from 4·7 to 7·3μ in length and 2·1 to 3·7μ in breadth.

Mode of infection

Mr Adams has kindly supplied us with the following information which involved the possible mode of infection with or transmission of *Thelohania corethrae* to new hosts. On 25 November 1938 he collected a large number of larvae of *Chaoborus flavicans* from the pond at Montreal West. Among them was the first infected individual. It and the uninfected larvae were kept together in the laboratory for several days. After removal of the infected one, no larva developed signs of infection, the normal ones eventually pupated and metamorphosed into adults. In November 1939, after breaking ice an inch thick on the same pond, a further batch of larvae was collected by sweeping with a net. Again, a single larva showed macroscopic infection. Its companions did not become infected. These observations suggest that disintegration of infected larvae may be necessary to liberate the spores of *Thelohania corethrae*, that the freed spores may need a resting period before they become infective, and that a fairly dense population of *Chaoborus*, living in close contiguity, may be necessary to ensure propagation of *Thelohania corethrae*.

Schuberg & Rodriguez (1915) in Germany kept infected larvae of *Corethra* (*Savomyia*) *plumicornis* in an aquarium with normal larvae. The ones infected with *Thelohania corethrae* gradually died, but the normal ones remained alive

until the following spring and showed no sign of infection. Transference of the contents of the aquarium to the original infected basin did not result in further infected larvae.

The German and Canadian experiences, then, agree in that infection did not occur, though normal and infected larvae coexisted. This may be because natural discharge of spores of *T. corethrae* did not take place. There was no evidence of aperture or point of discharge of spores in the case of the Canadian hosts, nor is there mention of such by the German workers. It is probable that liberation of spores from *Chaoborus* only occurs by the disintegration of the host. It is not definitely stated that the infected larvae of Schuberg & Rodriguez decayed in their aquarium. If not, spores may not have been liberated and, consequently, further infections did not develop.

Systematic position

The occurrence of *Thelohania* in insects was first noted by Hesse (1903*a*). *Thelohania corethrae*, parasitic in the larvae of *Corethra* (*Savomyia*) *plumicornis*, was first described by Schuberg & Rodriguez in 1915. These authors gave detailed accounts and illustrations of the schizogony and sporogony of the parasite. Most unfortunately, they gave no dimensions or scale of magnification whereby exact sizes could be calculated. Direct dimensional comparisons of *Thelohania corethrae* and the Canadian form, therefore, are not possible. But the morphological similarity of the two is striking. The spore of *T. corethrae* has one sporoplasmic nucleus, but karyogamy may have occurred. We also have seen spores with one sporoplasmic nucleus, though two were more common.

As far as we have been able to ascertain, the only other species of *Thelohania* from a Corethrid is that described by Lutz & Splendore in 1908 as *Nosema corethrae* from a species of *Corethra* (*Savomyia*) larva. The organism was certainly a *Thelohania*, as the authors describe cysts each of which contained eight spores. The spores were pyriform or curved cylinders in shape and were 5·5–7·5 by 1·5–2μ. Kudo (1924) transferred the *Nosema corethrae* of Lutz & Splendore to the genus *Thelohania* and renamed it *T. braziliensis*, as its exact identity with *T. corethrae* Schuberg & Rodriguez could not be established, owing to the incomplete descriptions of the Brazilian workers and the lack of dimensions of *T. corethrae*. Kudo remarks that *T. corethrae* is "doubtless a closely allied form". The spores of *T. braziliensis* Kudo are 5·5–7·5 by 1·5–2μ.

Morphologically, there are strong resemblances between the Canadian *Thelohania* from *Chaoborus flavicans* and *Thelohania corethrae* Schuberg & Rodriguez. The dimensions of the oval spores, 4·6–7·3 by 2·1–3·7μ, and the shape of the spores are different from those of *T. braziliensis*, the breadth in particular being greater. Comparing the morphology of the different stages of

our parasite with those of *T. corethrae*, it seems to us that the similarities are sufficient to justify us in considering the *Thelohania* of *Chaoborus flavicans* to be *Thelohania corethrae*, and as such we designate it. Dimensions of the different stages are now provided, together with a new host and extension of the range of *T. corethrae* to the North American continent.

Thelohania bracteata Debaisieux & Gastaldi, 1919

Syn. *Glugea bracteata* Strickland, 1913, and probably *Nosema simulii* y Lutz & Splendore, 1904.

Thelohania bracteata from larvae of *Simulium venustum* and *S. bracteatum*, has been under observation, infected specimens having been obtained at Rawdon, Lantier, near Quebec and near Gaspé, Quebec Province. One infected adult *S. venustum* also was captured near Gaspé. All the infections except those of the larvae captured near Quebec were slight.

Thelohania fibrata Debaisieux & Gastaldi, 1919

Syn. *Glugea fibrata* Strickland, 1913.

This parasite has been found in one larva of *Simulium venustum* from Gaspé, and in several preserved larvae, kindly sent to us from the environs of Quebec by Mr C. R. Twinn.

We have not observed *Thelohania multispora* Debaisieux & Gastaldi (syn. *Glugea multispora* Strickland).

The question of specificity among the species of *Thelohania* occurring in *Simulium* larvae is difficult and somewhat confused. Perhaps there may eventually prove to be only one species, with varietal differences due to the influence of different hosts, seasonal variation and the like. In this event, the priority of the name *Thelohania varians* Debaisieux, 1913, would have to be considered. Until morphological and seasonal variation in developmental stages, which may account for varying descriptions and occurrence of macro- and microspores, have been worked out, the species names *T. bracteata* and *T. fibrata* are retained.

Thelohania legeri Hesse, 1904

Thelohania legeri Hesse has been found in two out of seventy larvae of *Anopheles punctipennis*, collected near Saint Lambert, Province of Quebec. It has been reported by Kudo (1924, 1924*a*) from the same host in Illinois, U.S.A., and from larvae of *Anopheles barbirostris*, *A. fuliginosus*, *A. funestus* (*A. veruna*) *A. hyrcanus*, *A. ramsayi* and *A. subpictus* (*A. rossi*) in 1929. Two of us have also observed *Thelohania legeri* in larvae of *Anopheles gambiae* collected in Zululand. It is probably the most widely distributed species of *Thelohania*. Its development has been described by Hesse (1904*a*).

GENERAL REMARKS

The genus *Gurleya* is of interest in regard to the habitats of its hosts and host-specificity. Six species are known, five of which occur in western Europe and one in eastern Canada. *G. tetraspora* is parasitic in the Cladoceran, *Daphnia maxima*. *Gurleya legeri* has two hosts, the Ephemerid, *Ephemerella ignita* and a Trichopteran larva. *Gurleya francottei* parasitizes the Ptychopterid, *Ptychoptera contaminata*. *Gurleya richardi* occurs in a Copepod, *Diaptomus castor* and *Gurleya cyclopis* in another Copepod, *Cyclops albidus*. *Gurleya aeschnae* is parasitic in nymphs of *Aeschna grandis*, a member of the Odonata. The genus thus far is restricted to dipterous larvae and nymphs and to the Cladocera and Copepoda among the Crustacea. All the hosts have similar fresh-water habitats and, *Aeschna* excepted, are mainly or exclusively feeders on vegetation with its population of Sarcodina, Mastigophora and Ciliata. Similar habitats and habits may be expected to lead to infections with similar or identical parasites. The different species may have arisen by modification of a basic type by the action of the serum or haemocoelic fluids of the different hosts. Where the body fluids of hosts living in the same habitat are antagonistic, then a parasite may become restricted to one kind of host, in other words, host-specificity may arise.

Species of the genus *Perezia* occur in such widely different hosts as the Gregarine, *Lankesteria ascidiae*, itself parasitic in the Ascidian, *Ciona intestinalis*, and the Insecta. Four species are parasites of Diptera, *Perezia mesnili*, *P. legeri* and *P. pieris* being parasitic in *Pieris brassicae* and *Perezia pyrausta* in larvae of *Pyrausta nubilabis*. One species, *Perezia aeschnae*, occurs in the nymph of *Aeschna grandis*, a member of the Odonata. The habitats of the hosts of the species of *Perezia*, then, are very different—a parasite of a Gregarine of a marine Ascidian, which provides an interesting example of hyperparasitism, plant-feeding Lepidopterous larvae and carnivorous nymphs of Odonata. The wide differences in habits and habitats of the hosts coincide with differences in their parasitic *Perezia*.

Regarding *Glugea hertwigi*, the European form occurs in *Osmerus eperlanus*, an inhabitant of fresh water. In the United States it has been described from *O. mordax* from salt water. In Canada, it is now recorded from *O. mordax* from a riverine habitat. Its spores have also been figured by Bond from *Fundulus heteroclitus*, usually a fresh or brackish water dweller. The differences in morphology and in range of spore dimensions seem to reflect the effects of different hosts and host habitats, leading perhaps to isolation of different varieties, but more work, including experiments under natural conditions, on this interesting subject is needed.

The wide geographical distribution of *Thelohania legeri* has already been indicated. The possibility of *T. legeri* being regarding as a basic or central

form of the genus *Thelohania*, occurring in aquatic Diptera, from which species parasitic in other aquatic insect larvae and Crustacea have been derived, may be considered, especially in view of the similarity of habitats and habits of their hosts.

SUMMARY

An account is given of some Microsporidia found in certain fishes and insects in eastern Canada, among which are new species of *Nosema*, *Perezia* and *Gurleya*.

Nosema pimephales n.sp. produces large cysts or tumours in the abdomen of *Pimephales promelas*, one out of a large number from Lake Guindon, Province of Quebec, being infected.

Nosema branchiale Nemeczek has been observed from a cod, *Gadus callarias*. The organism is shown to be a *Nosema*, though the incomplete original description has caused doubts as to whether some other genus was involved. Further details are now given.

Nosema apis Zander and *N. bombi* Fantham & Porter have been found in Canada in hive-bees and humble-bees respectively, the latter being recorded from a new host, *Bombus vagans*.

Glugea hertwigi n.var. *canadensis* is described from *Osmerus mordax* from Lake Edward.

Perezia aeschnae n.sp. has been found in nymphs of the large dragonfly, *Aeschna grandis*, collected near Montreal and is described and illustrated.

Perezia legeri Paillot has been observed in larvae of *Pieris brassicae*.

These appear to be the first records of *Perezia* from insects in North America, and the zoogeographical distribution of the genus is extended to the Odonata.

Gurleya aeschnae n.sp. is described from a nymph of *Aeschna grandis*. It is the first species of *Gurleya* to be described from the Odonata and the first record of the genus from the North American continent.

Thelohania corethrae Schuberg & Rodriguez is described from the larvae of *Chaoborus flavicans*. Measurements of the parasite, which were lacking in the original description, are now supplied.

Thelohania bracteata from larvae of *Simulium bracteatum* and larvae and one adult *S. venustum* and *Thelohania fibrata* from larvae of *Simulium venustum* are recorded from places in the Province of Quebec. The need of reinvestigation of the species of *Thelohania* from various *Simulium* and the possibility of there being but one species, *Thelohania varians* Debaisieux, are indicated.

Thelohania legeri Hesse is recorded as a parasite of larvae of *Anopheles punctipennis* in Quebec Province and of *A. gambiae* in Zululand. It is probably the most widely distributed species of *Thelohania*, occurring in Anophelines in Europe, Asia, Africa and North America.

Some general remarks regarding zoogeographical distribution, habitat, host-specificity and possible origin of species and varieties in connexion with *Gurleya*, *Perezia* and *Thelohania* are presented.

ACKNOWLEDGEMENTS. Our grateful thanks are tendered to Mr J. R. Adams, M.Sc., for the infected larvae of *Chaoborus flavicans*, which he collected under very difficult conditions and sent to us, to Dr F. W. Edwards, F.R.S., for the identification of the *Chaoborus*, to Mr C. R. Twinn, M.Sc., for some preserved infected larvae of *Simulium*, which were of use for comparison with our freshly captured material, and to our fellow-members of the Montreal Branch of the Entomological Society of Ontario for identification of many insects for us.

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EXPLANATION OF PLATE V

All figures were drawn using an Abbé-Zeiss camera lucida.

Figs. 1–18. *Nosema pimephales* n.sp.

Figs. 1–7. Giemsa stain. ×1350.

Fig. 1. Small trophozoite.

Figs. 2–7. Various stages in schizogony.

Fig. 2. Binary fission with nuclear strand present.

Fig. 3. Binucleate schizont.

Figs. 4, 5. Stages in separation of daughter forms.

Figs. 6, 7. Clusters of meronts, some not completely separated.

Fig. 8. Multinucleate schizont. ×2600.

Figs. 9–18. Sporogony.

Fig. 9. Young spores. ×1350. Giemsa stain.

Figs. 10–18. Stages in spore formation. Iron haematoxylin. ×2600.

Fig. 10. Young spore showing one sporoplasmic, one capsulogenous and one parietal nucleus.

Fig. 11. Spore with compact capsulogenous nucleus.

Figs. 12–14. Spores showing vacuole and polar capsule with polar filament.

Figs. 13–17. Spores showing various appearances of polar filaments within the polar capsules. From sections of cyst.

Figs. 19–28. *Nosema branchiale* Nemeczek.

Figs. 19–27. ×2600. Fig. 28. ×1350. Stained methyl green.

Fig. 19. Young trophozoite.

Fig. 20. Binucleate schizont.

Figs. 21, 22. Tetrads of meronts produced by binary fission in two directions.

Fig. 23. Four meronts produced by division in one direction.

Fig. 24. Sporoblast showing two sporoplasmic, one capsulogenous and one parietal nucleus.

Fig. 25. Fresh spore, showing polar capsule and vacuole and outline of sporoplasmic nuclei.

Fig. 26. Spore showing nuclei.

Fig. 27. Spore showing nuclei and part of polar filament.

Fig. 28. Outline of spore with polar filament extruded under pressure.

Figs. 29–42. *Glugea hertwigi* n.var. *canadensis*.

Figs. 29–42. Iron haematoxylin. ×2600.

Fig. 29. Amoebula.

Fig. 30. Binucleate schizont.

Fig. 31. Schizont with two nuclei, one of which has nearly completed a second division.

Figs. 32, 33. Tubular multinucleate schizonts showing various stages of nuclear division without cytoplasmic cleavage.

Fig. 34. Two recently divided schizonts, each of which will ultimately form four uninucleate individuals.

Figs. 35–37. Sporonts with much less densely staining vacuolated cytoplasm.

Figs. 38–42. Spores showing details of structure. Fig. 42 shows the lateral position of the polar capsule.

Figs. 43–52. *Perezia aeschnae* n.sp.

Figs. 43–52. ×1350.
Fig. 43. Young binucleate trophozoite.
Fig. 44. Schizont with two groups of two nuclei.
Fig. 45. Schizont with binucleate daughter forms not yet separated.
Figs. 46–48. Elongating sporonts.
Fig. 49. Halter-shaped sporont.
Fig. 50. Sporont containing two spores.
Figs. 51, 52. Spores with polar filaments ejected under pressure.

Figs. 53–59. *Gurleya aeschnae* n.sp.

Figs. 53–59. ×1350.
Fig. 53. Binucleate tubular schizont.
Fig. 54. Pansporoblast with nucleus of large chromatin granules.
Fig. 55. Sporont with two nuclei.
Fig. 56. Sporont with four nuclei; cytoplasmic cleavage beginning.
Figs. 57, 58. Sporoblasts with four spores.
Fig. 59. Spore showing structure brought out by overstaining and progressively destaining.

Figs. 60–74. *Thelohania corethrae* Schuberg & Rodriguez.

Figs. 60–66. Schizogony. ×2600.
Fig. 60. Amoebula.
Fig. 61. Binucleate, oval young schizont.
Fig. 62. Schizont with nuclei migrating to poles.
Fig. 63. Schizont with two separate and one dividing nucleus. Cytoplasmic segregation beginning.
Fig. 64. Tetranucleate stage.
Fig. 65. Schizont with four clusters of two nuclei.
Fig. 66. Schizont forming cluster of eight binucleate meronts.
Figs. 67–74. Sporogony. Figs. 67–69, 72–74. ×2600.
Fig. 67. Binucleate pansporoblast. Alveolar or vacuolated pale staining cytoplasm.
Figs. 68, 69. Sporoblasts dividing.
Fig. 70. Sporoblast with four sets of two nuclei. ×1350.
Fig. 71. Sporoblast with eight sets of two nuclei around which cytoplasm is condensing. ×1350.
Fig. 72. Fresh sporoblast with eight spores.
Fig. 73. Stained spore showing vacuole, part of polar filament and two sporoplasmic nuclei.
Fig. 74. Spore with partly extruded polar filament.

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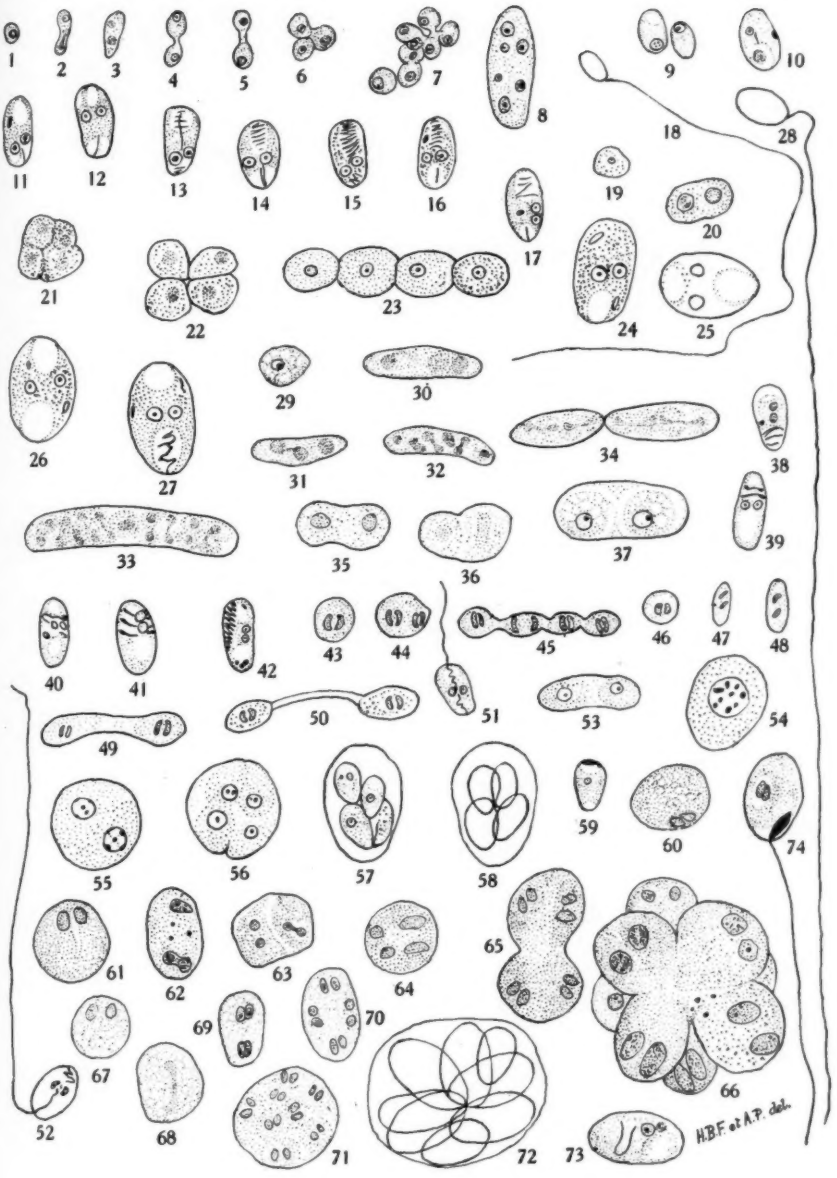

Figs. 1–18. *Nosema pimephales* n.sp. Figs. 19–28. *Nosema branchiale* Nemeczek. Figs. 29–42. *Glugea hertwigi* n.var. *canadensis*. Figs. 43–52. *Perezia aeschnae* n.sp. Figs. 53–59. *Gurleya aeschnae* n.sp. Figs. 60–74. *Thelohania corethrae* Schuberg & Rodriguez.

UNIV. OF MICH.

A RECORD OF TREMATODE PARASITES FROM *MOLA MOLA* AND *RANICEPS RANINUS* (LINN.)

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While making a survey of the parasites of littoral fishes at Cullercoats, Northumberland, parasites from *Mola mola* and *Raniceps raninus* came into my possession. These fishes are rarely found in British waters and so far no parasites have been recorded from *R. raninus* in British waters.

Tristomum molae Blanchard, from **Mola mola**

In October 1938 I was given thirty-two specimens for identification by Prof. A. D. Hobson, who had obtained them from a specimen of *Mola mola*, the sunfish, which had been landed at Seahouses, Northumberland.

When taken from their host they were a pale cream colour and varied in size from 1·2 to 3·0 cm. diameter. They were identified as *Tristomum molae* Blanchard. This species is easily distinguished from other species of *Tristomum* by the formation of the large sucker, the bars uniting the seven rays not forming a true heptagon. Usually the anterior bar is placed nearer the oral suckers. There was variation in the position of this bar in some specimens, the sucker appearing to be turned 60° to the right or left in some forms.

This species has only once before been recorded from British waters (Southern, 1911), in the locality of the west coast of Ireland, the parasite being collected from the gills of *Mola mola* while the present specimens came from the skin of the body.

Tristomum molae Blanchard seems to have been described under several names, and a survey of the literature indicates that *T. cephala* Risso, *T. aculeatum* Couch and *T. rudolphianum* Diesing are synonyms of *T. molae*. This confusion has probably been due to the rather poor description given by Blanchard in 1847, which makes it difficult to distinguish *T. molae* from *T. coccineum* Cuvier. The diagrams do not indicate any difference in the formation of the suckers. Saint-Remy (1898) has given a key which clearly separates these two species.

Nicoll (1915), in his list of Trematodes of British fishes, includes *T. cephala* Risso and *T. rudolphianum* Diesing as having been found on fishes which occur in British waters, but lists the parasites as not having been found in these waters.

It may be noted that Nicoll includes *T. coccineum* Cuvier and *T. papillosum*

Diesing in his list. Study of the literature indicates, however, that these two species are synonymous (Monticelli, 1889; Saint-Remy, 1891, 1898; Setti, E., 1899).

Helicometra pulchella (Rud.), from **Raniceps raninus** (Linn.)

In February 1940 Mr T. W. Burdon, B.Sc., collected a specimen of *Raniceps raninus* (Linn.) from the beach at Cullercoats and in its intestine were found two trematodes. These were given to me and identified as *Helicometra pulchella* (Rud.). This parasite has previously been recorded from *Labrus berggylta, Conger conger, Trigla pini, Gobius paganellus, Blennius pholis* and *gattorugine, Lepidogaster gouanii, Labrus mixtus, Ctenolabrus rupestris, Zeugopterus punctatus* and *Anguilla vulgaris*, but has not been recorded from *Raniceps raninus*, and, to my knowledge, no parasite has been recorded from *Raniceps* in British waters. *Podocotyle atomon* (Rud.) is recorded from this fish in Nicoll's list of trematode parasites from British marine fishes outside British waters.

The specimen in my possession agrees with the description given by Nicoll (1910). Examination of the testes shows the multilobed condition described by Nicoll. Details, which correspond closely with those given by Nicoll (1910), are shown below:

	Present specimen in mm.	Nicoll's specimen in mm.
Length	2·0	2·5
Maximum breadth	0·69	0·83
Suckers	Globular	Globular
Diameter of oral sucker	0·2	0·23
Diameter of ventral sucker	0·31	0·35
Diameter of pharynx	0·09	0·1
Testes	Tandem and contiguous Multilobed	Tandem and contiguous Multilobed
Breadth of testes	0·32	0·37

The yolk glands in the post-testicular space are as described by Nicoll.

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CASUAL BEDS AS A SOURCE OF LOUSE INFESTATION

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In a paper at present in the Press, we have endeavoured to show that where moderate or high infestations of men with *Pediculus humanus corporis* are present, the maintenance of these, and the level at which they tend to remain, are not dependent on the environment of the infested subject. The degree of infestation is a reflexion of the subject's recent standards of personal hygiene, and his habits at a given moment mould the structure of his infestation in the future.

The genesis of his infestation, however, is independent of the individual; in this respect at least he is purely a victim of his environment. The sources of initial infestation are usually classified together as "a verminous environment"; details of the relative importance of each constituent are practically unknown. Where men are huddled together for comfort or warmth and are unable to exercise strict personal cleanliness, e.g. in dug-outs, infestation will spread from one infested subject in the group (Peacock, 1916). According to Nuttall (1917), bedding and blankets are a fruitful source of infestation. Peacock (1916) believes, on the other hand, that blankets are not important as a means of dissemination. Hamer (1910) found that the number of verminous beds in London common lodging houses ranged from 31% in winter to about 12% in June. Examinations over the years 1910–16 (reported by Nuttall, 1917) showed that these figures were not again attained, the highest infestation for any month during this period not exceeding 8% of the beds examined.

In the course of experiments on control of the body-louse under natural conditions, the authors had opportunities of making contact with both the inmates and staff of several common lodging houses in the East End of London; the information given below relates to one of these.

The hostel was run by the Salvation Army, and was rather above the general average for such hostels in the East End. The dormitories were airy and well lighted. The beds were examined daily by the staff, and any sheets soiled or noticed to be verminous were changed. The sheets were changed each fortnight, i.e. each week one of the two sheets was changed.

During April 1940, the under-garments of sixty-five of the inmates were examined. Thirteen, i.e. 20% of the sixty-five, were found to be free from lice. Of the fifty-two infested cases twenty-four had totals of between one and ten lice only. That is, relative to that in other common lodging houses examined, the degree of infestation of the occupants of this hostel was low (MacLeod & Craufurd-Benson, in the Press).

During May, an opportunity was obtained of examining the beds in three of

the dormitories. An experiment was arranged in which each alternate bed was dusted, immediately after the sheets were changed, with a preparation which it was hoped would prevent the bed becoming infested. A week later, immediately prior to the next routine changing of sheets, each bed was carefully scrutinized, and the presence, number and stage of any lice recorded. Actually, no difference was observed between the infestation of the treated and control beds, the preparation having apparently had no appreciable effect. The results for the treated and control beds have, therefore, been combined, to simplify presentation of the data.

The gross results were as follows:

Dormitory	No. of beds	No. infested	Percentage
A	84	27	32·2
B	83	11	13·3
C	35	11	31·4
Total	202	49	24·3

These percentages are open to misinterpretation, from several causes. Thus, some of the beds had not been occupied during the previous week, some had been occupied for one only of the preceding 6 days, and so on. The dormitory records were obtained, and the gross figures are corrected in the accompanying table, which gives the numbers of infested beds, grouped according to the number of nights on which they had been occupied.

		No. of nights on which beds were occupied							No. of beds occupied for 4 or more nights
	Dormitory	0	1	2	3	4	5	6	
A	No. of beds	—	2	13	6	5	11	47	63
	No. infested	—	1	1	—	3	4	18	25, i.e. 39·7%
B	No. of beds	12	9	10	6	8	9	29	52
	No. infested	—	—	—	1	2	1	7	10, i.e. 19·2%
C	No. of beds	—	—	3	1	3	6	22	31
	No. infested	—	—	1	—	—	3	7	10, i.e. 32·2%
	Total beds	12	11	26	13	16	26	98	140
	No. infested	—	1	2	1	5	8	32	45, i.e. 32·2%

It will be observed that except for four instances, the infestations occurred in those beds occupied for more than half the week, i.e. the more frequently a bed is occupied, the greater is the probability of its being infested.

There is an interesting suggestion, from the individual figures, that if the beds be left empty for one or two nights, their infestations tend to disappear. Thus, three of the beds occupied for five out of six nights and nine of those occupied for four nights were empty on the final night; of these twelve only one was infested. The corresponding numbers empty on any other one night of the six, total to seven and twenty-three respectively. Of these thirty, eleven, i.e. the normal infestation incidence of one to three, were infested.

Unfortunately, of the forty-five infested beds occupied for four or more nights, not one was empty for two successive nights. The effect of two successive unoccupied nights can therefore only be assessed from the meagre total of 4 positive cases—those occurring in the beds occupied for three or less nights.

Of twenty instances where the bed was empty for the last two nights, but occupied on three of the remaining four nights, none was positive, whereas, of twenty-eight instances where the bed was empty for the first two nights, plus any one other night, three were positive.

The suggestion contained in these results, namely that beds can be deloused by being left vacant for a day or two, deserves further investigation. It does not necessarily conflict with Peacock's record of only ten blankets out of twenty-five being free of lice when examined after being 4 days away from infested men, for the actual total of lice counted was five alive and twenty-one dead, i.e. an average of only one living, and possibly moribund, louse in every three infested blankets.

Of the forty-nine infested beds, forty-three upper sheets, eighteen lower sheets and three pillows were infested. The age distribution of all the lice found was ninety-seven adults and 219 larvae. The frequency distribution of infestations was:

1	2–3	4–6	7–10	11–18	Over 18
17	12	10	6	2	2

The highest infestation, 117 lice, was found in a bed which had been slept in for only one night that week, on the night prior to examination.

When the beds were treated, and a week before the main examination, a cursory examination of each was made, and seventeen of them were noticed to be infested. The numbers of these beds were noted. Ten of them were control beds, and of these, only five were still infested a week later. They had all been slept in for four or more nights. Similarly of the seven treated beds, all of which had been slept in for four or more nights, only three were still infested at the main examination.

It seems a reasonable assumption that in many of these cases of disappearance of infestation the lice had been carried away by one or more of the bed occupants during the intervening 6 days. Such a transfer would ordinarily be expected to be obscured (*a*) by failure of all the lice to transfer to the bed occupant, and (*b*) by the reverse transfer of lice to the bed by one or other of the occupants. The fact that the above evidence of transfer to bed occupants was obtained, in spite of the unlikelihood of demonstrating such transfer, would seem to be significant of the major importance of casual beds as a source of infestation.

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OSMOTIC RELATIONS OF SOME METAZOAN PARASITES

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Introduction

The problem of the osmotic relations of parasites has received little attention. Excepting the very valuable work of Schopfer (1932) on some common helminths of vertebrates, investigations on this aspect of host-parasite relationship based upon direct measurements of osmotic pressure do not seem to have been made. It is well known that many parasites are subjected to profound changes in environment during their life history. Many of them in their adult stages are apparently indifferent to osmotic and ionic changes taking place in their surrundings. Those living in the blood and muscles of their hosts have more or less osmotically stable surroundings of a fairly high concentration, and osmoregulation is not so important in them as in those living in the alimentary canal of their hosts. The external parasites of aquatic animals which are exposed to the same medium as their hosts have to regulate their body fluids in accordance with the surrounding medium; those which are not specialized in structure or only semi-parasitic would probably show the same type of osmotic behaviour as their non-parasitic relatives. Many of the external parasites are, however, permanently attached and highly specialized in structure; normal respiratory, vascular and excretory systems are either absent or degenerate. In them the mechanism of regulation is by no means simple.

We report in this paper the results obtained with three parasites of widely different habits: (1) a parasitic nematode from the alimentary canal of a reptile; (2) a blood-feeding copepod from gadoid fishes; and (3) a blood-sucking isopod from a prawn. These results, though only of a preliminary character, appear to be helpful in understanding their osmotic relations with their hosts.

Measurements of osmotic pressure were made by Baldes' (1934) modification of the Hill thermoelectric technique. Details of procedure have been described in another paper (Panikkar, 1940*b*), and the particular method employed with each parasite is given in the appropriate section below.

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I. **Angusticaecum** sp. (Fam. Heterocheilidae: Nematoda) from **Testudo graeca** (L.).

The tortoise was received for autopsy 3 days after its death (28 April 1940), which occurred soon after its emergence from a long period of hibernation. Fourteen of these relatively large nematodes were found, causing a marked obstruction of the colon, together with several hundred small oxyurids; nearly all worms were alive and active and they were transferred immediately to tap water and rinsed. Since *Angusticaecum* sp. were still active in tap water on the following day, it was decided to use them for studying their osmotic behaviour. Some specimens were accordingly left in tap water for three more days and the remainder were put into experimental media (0·9 % NaCl; approx. 50 % sea water; and sea water). Those worms destined for the more concentrated media were allowed to remain in each of the less concentrated for 15 min., so that the transition was a gradual one. On the second day the 0·9 % NaCl medium became contaminated and all the worms died and had to be discarded; those in the other media remained actively moving. On removing a worm for experiment it was rapidly wiped with filter paper, and it was possible to extract ample body fluid by means of micropipettes for at least two osmotic pressure determinations, the mean of which is cited in the accompanying table.

Table 1

Worm no.	Length in mm.	Experimental media and time therein	Final medium	Osmotic pressures: as % NaCl		
				Medium	Body fluid	Difference
1	104♀	Tap water for 4 days	Tap water	0·001	1·280	+1·279
2	62♀	Tap water for 4 days	Tap water	0·001	1·157	+1·156
3*	71♂	Tap water for 1 day then sea water for 4 days	Sea water	3·510	3·535	+0·025
4	84♀	Tap water for 1 day then diluted sea water 5 days	Diluted sea water	1·852	1·994	+0·142
5	104♀	Tap water for 1 day then diluted sea water for 5 days	Diluted sea water	1·852	1·932	+0·080
6	87♀	Tap water for 5 days then ligatured in it and into sea water for 1 day	Sea water	3·510	1·996	−1·514 (ligatured part)
7	104♀	Tap water for 1 day then diluted sea water for 5 days in which ligatured and then back to tap water for 1 day	Tap water	0·001	1·025	+1·024 (unligatured part)
				0·001	0·978	+0·977 (ligatured part)

* This worm was in a moribund condition for 3 days after being transferred to sea water. It was infected with a pinkish bacterial growth on the cuticle round its anterior third; later, large white colonies of another type of bacterium made their appearance in this area. The activity of the worm was much reduced.

The value of 1·16 to 1·3 % NaCl for worms (nos. 1 and 2) which were kept in tap water for 4 days is clear evidence of their ability to maintain a marked hypertonicity in very dilute media; i.e. like freshwater animals they can maintain a high concentration of body fluid in media containing little or no salt. In environments of higher osmotic pressures (nos. 3, 4 and 5), there is a corresponding increase in the value for body fluid and a state of approximate isotonicity is reached in sea water of 3·51 % NaCl. A slight hypertonicity exists in an external medium of 1·852 % NaCl. The shape of the osmotic pressure curve which one might obtain, as judged from these results, would not be unlike that of euryhaline invertebrates, such as *Carcinus maenas* and *Nereis diversicolor* (*vide* Krogh, 1939), which conform to the rule of isotonicity of external and internal media in sea water, and progressive hypertonicity of body fluid in lower concentrations of the external medium. Similarly *Angusticaecum* sp. appears unable to prevent rise in osmotic pressure when concentration of the external medium is raised; and it may be concluded that a mechanism for maintaining a body fluid concentration hypotonic to the external medium has not been developed.

The rise in osmotic pressure when worms are transferred to sea water may be brought about by the passage of salts through the body wall or by the absorption of salts through the gut wall. To exclude the latter possibility, a worm was carefully ligatured at both ends (no. 6) in tap water, wiped with filter paper and then transferred to sea water; after the lapse of a day the osmotic pressure of the body fluid was found to have risen from the normal in tap water (see nos. 1 and 2) of 1·2 to about 2·0 % NaCl. Similarly in no. 7, which was ligatured in dilute sea water of osmotic pressure 1·85 % NaCl and had an osmotic pressure of about 1·9 % NaCl, the value fell to about 1·0 % a day after transference to tap water. In neither worm was there any appreciable swelling or collapse of the body wall between the ligatures. These conditions could be brought about by the passage of water alone or by the passage of water and salts through the body wall. The ligatured part of worm no. 7 would certainly have been markedly swollen, however, if sufficient water had passed through the cuticle to reduce the osmotic pressure to the observed value. Worm no. 6 showed no appreciable loss of turgidity in the ligatured part. The observed differences in osmotic pressure in worms nos. 6 and 7 cannot therefore be accounted for entirely by the passage of water through the cuticle, but must also be, in part, due to the passage of ions in each direction through the cuticle. This must, however, be very slow, as shown by the difference between external and internal media even after 24 hr. Information is lacking as to the percentage contribution of chlorides to the total osmotic pressure of the body fluids of parasites in normal circumstances. That chlorides and other ions in sea water may represent over two-thirds of the total osmotic pressure under artificial conditions of hypertonicity may be inferred from our

experiments. It will be recalled that these worms had all been left in tap water for at least 24 hr., during which time it may be assumed that there was a maximum leaching-out of solutes to which the cuticle is permeable, leaving a residual osmotic pressure of approximately 1·2 % (expressed in terms of NaCl); the increment of osmotic pressure in worms nos. 3, 4, 5 and 6 is thus entirely represented by ions acquired from the media: in no. 3 the increment is over 65 % of the total osmotic pressure. Mueller (1928) has demonstrated that the cuticle of ascarids is permeable (i.e. in the outward direction) to urea, potassium iodide and certain aniline dyes (neutral red and methylene blue), but that glucose in the small concentrations normally present in the worm does not pass out; there was, however, some outward passage when high concentrations were introduced into the cuticle when this was used as a dialysing membrane, as he employed it in these investigations.

Our results are in general agreement with those obtained by Schopfer (1932) and by Vialli (1923, quoted by Schopfer, 1932). With body fluids or with extracts of *Ascaris* spp. from certain mammals Schopfer obtained freezing-point depressions varying between −0·62 and −0·78° C. (about 1·2–1·4 % NaCl) in external media (intestinal fluids of the respective hosts) of Δ −0·75 to −1·0° C. *Proleptus obtusus*, living in the alimentary canal of a marine elasmobranch *Scylliorhinus* sp., showed a Δ of −2·55° C. in an external medium of Δ −2·40° C. He takes these results and those from other common helminths studied in support of his contention that the body fluids of helminth parasites are nearly isotonic with their natural media, and that the latter are always slightly more concentrated. Unfortunately we have no data on the osmotic pressure of the intestinal contents of the tortoise; the experimental evidence, however, suggests that *Angusticaecum* sp. is poikilosmotic in higher concentrations of the external medium.

In the same paper Schopfer describes a series of experiments designed to indicate the osmotic response of *Ascaris megalocephala* (from the horse) to media of varying hypo- and hyper-tonicity. He removed worms from the experimental media at regular intervals and noted the increment and decrement in weight; in most media he found that equilibrium was attained within about 5 hr. From this relatively rapid accommodation and the shape of the weight curves, he infers that parasitic helminths have an osmotic behaviour similar to that of marine invertebrates, that the cuticle is readily permeable to water in both directions and also that the response to hypotonicity is more rapid than that to hypertonicity.

Schopfer's worms were, however, unable to survive immersion in tap water: he observed a marked swelling followed by a prolapse of the uterus through the genital pore, and in some worms the cuticle burst as a result of the increased hydrostatic pressure from within. This marked difference in behaviour from our specimens may be due to the experimental treatment of the latter or to a

peculiarly low permeability of the cuticle, or again to some special adaptability in the helminths of this host; for conditions in the tortoise may well be more rigorous than those in the gut of a mammal such as the horse. The physiology of the tortoise is characterized by a strict economy of water: for instance, it is well known that its excreta are highly concentrated, and further, the special conditions existing during hibernation may require some additional resistance on the part of the worms.

We have little precise knowledge of the osmoregulatory organs of helminths, and of the mechanism whereby the infective stages and early larvae adapt themselves to their varying habitats. Working with cercariae of trematodes Herfs (1922) and Westbald (1922) have shown that a correlation exists between the rate of contraction of the excretory vesicle and the osmotic pressure of the surrounding medium. Since the amount of excretory fluid discharged is definitely higher when they are in fresh water than when they are in salt water, it is very likely that the excretory system of trematodes has an osmoregulatory function. The so-called "excretory system" of nematodes has been re-examined by several workers recently and Mueller (1928) has shown conclusively that it is not excretory in function but secretory, and that, in many species, it is subservient to feeding: accordingly, it is not likely to have an osmoregulatory rôle. The means which forms like *Angusticaecum* sp. have for enduring tap water for long periods remains unknown, for the relative part played by low permeability and active ion-absorption (Krogh) in these worms is not clear.[1]

II. **Lernaeocera branchialis** (L.) (Fam. Lernaeoceridae [=Lernaeidae]; Copepoda) from **Gadus** spp.

Lernaeocera branchialis (L.) is a common copepod which occurs on many species of gadoid fish, feeding on the blood of the host. The large females of this parasite are found attached near the anterior angle of the 4th gill arch of the fish, the head, part of the neck and antler-like outgrowths of the thorax being imbedded in the heart, ventral aorta and adjacent tissues. The copepodid larval stages of males and females occur on the gills of certain flat fishes which act as intermediate hosts before the parasites finally settle on gadoids. A summary of our knowledge of the structure and bionomics of *L. branchialis* is given by Wilson (1917) based mainly on the work of Scott (1901) and other authors, and some aspects of its structure and physiology have been investigated more recently by Schuurmans Stekhoven jr. (1936) and Schuurmans Stekhoven jr. & Punt (1937). At Plymouth, the species is frequently seen

[1] In his recent book on osmotic regulation in aquatic animals (1939) Krogh has unfortunately overlooked the papers by Mueller and Schopfer, and he mentions that because nematodes have a very thick cuticle, it is natural to suppose that its permeability to water is exceptionally low. This is likely to cause misunderstanding since the general nature of semi-permeability of the cuticle of ascarids has been shown by both the authors cited above.

on the pollack (*Gadus pollachius*) and the whiting (*Gadus merlangus*), but only occasionally on the cod (*Gadus morrhua*) and the poor cod (*Gadus minutus*).

Since the adult females are firmly and permanently attached, the body fluid was removed from them *in situ*, the parasite being exposed by the rapid removal of the three overlying gills of the fish. The swollen genital segment was carefully wiped with strips of filter paper, and by introducing a fine glass canula it was possible to obtain a sufficient quantity of body fluid for two or three estimations of osmotic pressure. The risk of puncturing the alimentary canal was avoided by manipulating the animal in the field of a binocular microscope. The intestinal wall is extremely thin, being composed of a single layer of epithelial cells and a thin layer of transverse muscle fibres (Schuurmans Stekhoven jr. & Punt, 1937); it is therefore unlikely that great differences between the osmotic pressure of the intestinal contents and the body fluid of the parasite can permanently exist. In three experiments the parasite was excised with the surrounding tissues, so that the lumen of the heart and blood vessels of the host, where the mouth is imbedded, was open to the media in which they were placed. Only those specimens which were alive and healthy, as evidenced by the peristalsis in the gut, were used. The mean values obtained in the experiments are given in Table 2 below.

Table 2. *Determinations of the osmotic pressure* (*as percentage* NaCl) *of* Lernaeocera branchialis *under different conditions*

Expt. no.	Date (1940)	*Lernaeocera* body fluid	Osmotic pressure difference *Lernaeocera*/medium	Osmotic pressure medium	Time in medium hr.	Remarks
1	25 June	2·003	−1·507	3·510	—	5 hr. after death of host
2	25 June	2·027	−1·483	3·510	—	5 hr. after death of host
3	9 August	2·604	−0·856	3·460	—	2 hr. after death of host
4	12 August	2·854	−0·646	3·500	—	Host alive
5	10 May	3·498	+0·018	3·480	24	Kept *in situ* at 2° C. for 7 days; excised; then kept in sea water for 24 hr.
6	20 May	3·337	+0·047	3·290	168	Excised fresh; then kept in sea water 7 days
7	10 August	2·475	+0·232	2·243	24	Excised fresh; then kept in diluted sea water 24 hr.

Note. *L. branchialis* was taken from *Gadus pollachius* in all the above experiments except no. 5, where the host was *G. merlangus*. The excised parasites were kept in running sea water.

The body fluid of *Lernaeocera branchialis* while still attached to its host is found to have an osmotic pressure of 2·0–2·9 % NaCl, and therefore definitely hypotonic to the external medium when the latter is sea water. This range of variation is rather high, but is significant (compare below). When the parasite is excised and kept alive, isotonicity with the medium is reached when the latter is sea water and slight hypertonicity when it is diluted sea water. In experiments 5–7 osmotic equilibrium between external and internal media

may possibly have been brought about by the parasite taking in some of the surrounding medium through the mouth in place of the host's blood.

With only a few exceptions, marine invertebrates living in sea water are more or less isosmotic with their surroundings. *Lernaeocera*, though its body is bathed by sea water, is perpetually irrigated by the blood of the host, which is taken through the suctorial mouth. Unlike that of marine invertebrates, the blood of teleosts is markedly hypotonic to sea water. The close relationship between the blood of *Lernaeocera* and that of its host would appear to be the cause of its hypotonicity to the external medium.

We have measured the osmotic pressure of the blood of *Gadus pollachius* and found it to be equivalent to 1·443 % NaCl in an external medium (sea water) of 3·329 % NaCl. Three other gadoids investigated by Dekhuyzen (1904)—*Gadus morrhua*, *G. merlangus* and *G. virens*—have an average value of about 1·3 % NaCl (calculated). Even the lowest value obtained for the body fluid of *Lernaeocera* is considerably higher than these values. It is interesting to find, therefore, that though this parasite is hypotonic to sea water it is hypertonic to its host's blood. The parasite is thus seen to represent a complex osmotic system: surrounded as it is by a hypertonic medium and taking into its alimentary canal a hypotonic fluid (the host's blood) from time to time. It does not seem to have any osmoregulatory organ. The possibility of any rapid passage of substances through the body wall would appear to be precluded by its low permeability. It is probable, however, that water is slowly yet steadily lost from *Lernaeocera* into its hypertonic surroundings by osmosis, thus tending to make the body fluid more concentrated than the blood of its host. This would mean that every meal of blood from the host is followed by osmotic changes, and that the osmotic pressure of the body fluid of the parasite is constantly influenced by the quantity of host's blood in its alimentary canal and by the time which that blood has remained there. This explanation may be offered to account for the high range of variation of osmotic pressure actually observed in this parasite (experiments 1–4).

The values of osmotic pressure in normal and experimental animals have shown that the parasite is capable of living under widely varying conditions of *internal* osmotic pressure—from 3·5 to about 2·0 % NaCl. It is possible that soon after a meal the value may be even lower. The tissues must be able to maintain activity in a medium possibly as dilute as that of the host's blood. This remarkable tolerance to osmotic changes seems to have some bearing on its ability to survive when its host migrates from inshore waters up estuaries and again out to sea. Many gadoids live in inshore waters or in estuaries during part of their early life and living *Lernaeocera* are often found on fish taken from such habitats. It would be interesting to know the limits of salinity tolerance of the adult *Lernaeocera* on its host, and also of its early stages on the flounder (*Pleuronectes flesus*) which occurs in both fresh and salt waters.

III. **Bopyrus squillarum** Lat. (=**B. fougerouxi** G. et Bonn.). (Fam. Bopyridae; Isopoda) from **Leander serratus** (Penn.).

Bopyrus squillarum is a parasite of the common prawn *Leander serratus*, living attached to the branchial shield and feeding upon its host's blood. The large females (along with the minute males) are lodged in a hollow projection of the branchiostegite, to the inner lining of which the whole ventral surface of the parasite is closely adherent; the dorsal surface is thus freely exposed when the branchiostegite is cut off. By introducing a glass cannula between the tergites (which had been previously wiped with filter paper), a sufficient quantity of body fluid could be removed for making three osmotic pressure determinations. The means of the values obtained in each experiment are given in Table 3.

Table 3

Expt. no.	Date (1940)	Osmotic pressure: % NaCl		Difference in % NaCl between body fluid and external medium
		Bopyrus	External medium	
1	1 March	3·386	3·410	−0·024
2	21 August	3·072	3·290	−0·218
3*	21 August	3·296	3·290	+0·006
4	17 September	3·230	3·350	−0·120
5	17 September	3·280	3·350	−0·070

* Parasite was isolated and kept in sea water for 25 min. In all the other experiments body fluid was taken with the parasite *in situ* on the living prawn.

The osmotic pressure of *Bopyrus* from prawns living in sea water is found to vary between 3·0 and 3·4 % NaCl. The difference between the external and internal media in each experiment indicates that the parasite is nearly isotonic with the external medium, though with a marked tendency towards hypotonicity, which in no. 2 was to the extent of 0·218 % NaCl. In no. 3 the parasite was isolated from the prawn and kept in sea water, and isotonicity was observed in less than half an hour.

It has been shown that *Leander serratus* is hypotonic to the external medium when in sea water, the blood having an osmotic pressure varying from 2·6 to 2·9 % NaCl (Panikkar, 1940*a*). It is probable that as in *Lernaeocera*, the slight hypotonicity of *Bopyrus* is caused by the low osmotic pressure of its host's blood, which is its only source of food, and the comparatively low permeability of the integument.

Most species of *Leander* have remarkable powers of toleration to salinity changes in the environment and it would appear that this ability is also shared by *B. squillarum*, though in a less marked degree. *B. squillarum* var. *bimaculatus* is very common in the estuarine waters of the Gangetic delta (Chopra, 1923), and there are records of the species from the Black Sea (Rathke, quoted by Chopra). At Plymouth *B. squillarum* occurs mainly in inshore waters where

the salinity is not as high as in the open sea. Closely related bopyrids of the genera *Probopyrus* and *Palaegyge* occur only in fresh or brackish water. A mechanism of osmoregulation must certainly be evolved in them. It is likely that the blood of the host is the main source of chloride whereby hypertonicity is maintained when they are in media of low osmotic pressure. In these fresh water parasites, the host's blood would then be equally necessary for osmoregulation and for nutrition.

Finally, according to Mathias (1938), *Leander squilla* parasitized by *Bopyrus* is less resistant to the dilution of the external medium than non-parasitized prawns. Owing to the difficulty in obtaining a large number of infected prawns, we have not been able to verify his results in regard to *L. serratus* or to find the limits of salinity tolerance of the parasite at Plymouth.

Summary

1. The osmotic behaviour of three parasites in normal and experimental media has been studied with a view to understanding the relationship with their hosts.

2. *Angusticaecum* sp., a nematode from the intestine of the tortoise, is hypertonic in media of very low concentrations (1·1–1·3 % NaCl in tap water), but becomes isotonic in sea water and slightly hypertonic in 50 % sea water. Ligaturing experiments show that its cuticle is permeable to water and probably to salts.

3. *Lernaeocera branchialis*, a blood-feeding copepod from *Gadus* spp., is hypotonic to the surrounding sea water so long as it remains attached to its host, its blood showing an osmotic pressure equivalent to 2·0–2·8 % NaCl. Isotonicity with the medium is established when the parasite is excised and kept alive. Hypotonicity of *Lernaeocera* is probably caused by the low osmotic pressure of the blood of its host (1·443 % NaCl in *Gadus pollachius*), to which it is permanently attached.

4. *Bopyrus squillarum*, a blood-sucking isopod from *Leander serratus*, is isotonic or slightly hypotonic to sea water, the tendency towards hypotonicity being probably the result of the hypotonic nature of the blood of the host.

5. The osmotic properties of *Lernaeocera* and *Bopyrus* would suggest their ability to survive in dilute sea water, a fact which is supported by their occurrence on hosts living in inshore or estuarine habitats.

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STUDIES ON POPULATIONS OF HEAD-LICE (*PEDICULUS HUMANUS CAPITIS*: ANOPLURA)

IV. THE COMPOSITION OF POPULATIONS

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From the London School of Hygiene and Tropical Medicine

(With 4 Figures in the Text)

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The material

The previous papers in this series (Buxton, 1936, 1938*b*, 1940*a*) have described a method by which head-lice may be removed from a crop of hair and counted. In those papers the material was considered from the human point of view, that is to say, material from seven or eight different places was discussed: it yielded information about the incidence of infestation and its relation to the human being's age, sex and race, also to the season of the year, etc.

So far no attention, except for one brief note (Buxton, 1937), has been given to the strictly entomological side of the matter, and we will now consider the composition of the louse populations. For each infested head we know the total number of lice and the number of the males, females[1] and larvae. In dissolving the hair eggs are destroyed and we know nothing of their numbers. One assumes that all the insects in the crop of hair were alive at the time the head was shaved: this entails a small error, for it is evident that at death a louse might remain for some time among the hair. This source of error does not appear to be important, for if one examines infested heads one seldom finds a dead louse among the hair. The large collection of specimens from Cannanore has been preserved so that one could also identify and record the

[1] It will be remembered that the hair is dissolved and only the cuticle of the lice left for counting and examination, which is generally done at a magnification of ×8. It is possible that specimens showing a minor degree of intersexuality may have passed undetected. No gross intersexes, such as those figured by Keilin & Nuttall (1919), have been seen, and I am confident that they could not have passed unobserved.

separate larval instars: this is laborious and has in fact only been done for a part of the material. But in dealing with specimens for the other localities no attempt was made to identify separate larval instars. It will therefore be seen that the material available may be expected to yield information about the proportion of the sexes in natural populations and the number of young per parent: it may also be possible to obtain some indirect information about larval mortality.

The mass of information which is available is considerable, for it includes every infested head in the material which was the subject of the three previous papers. Even if we exclude the data from Jerusalem for reasons already explained (Buxton, 1938*b*) we have a total of 858 infestations for study. As Table 1 shows, almost exactly two-thirds of these contained only from 1 to 10 lice, nearly one-third from 11 to 100 and a very small proportion more than 100 lice.

One is probably not justified in lumping together facts collected from the different places. If we are to study the places separately we need give little attention to Sokoto and Nairobi, from which small numbers of infested heads and of lice were received: the collection from Lagos was derived from few heads but it contained larger numbers of lice: the collection from Colombo was extensive, but for reasons already given (Buxton, 1938*b*) it is necessary to disregard the number of larvae, so that it is only valuable where adults are concerned: one is left with the collections from Kakamega and Cannanore, both of which were well collected and contained large numbers of infested heads and of lice: it will be seen that the total number of heads from Cannanore exceeds the whole of the rest of the material. It has been shown (Buxton, 1940*a*) that infestation rates are very different in religious communities in the Cannanore material: it therefore seems best to confine one's work to the Hindus, discarding Moslems and Christians: one loses only sixty-six (12·1 %) infested heads.

This is perhaps a convenient place for recording that a heavily infested shirt from south London was found to contain 369 adult body lice, of which 177 (47·9 %) were males.

Previous writers have had relatively so little material that I have not attempted to compare their results with my own. The results of examining a few populations of *P. humanus* are given by Nuttall (1917, 1919) and by Awati (1922).

PROPORTION OF THE SEXES

It will be remembered that in certain strains of lice there is a tendency to produce families which are nearly or completely unisexual. This perhaps explains the remarkable disparity between the sexes which may be observed among the lice on a single head, particularly when the total number is low: it is reasonable to attribute this disparity to a head being nearly or entirely

populated by the progeny of one pair of lice. The following examples, which are extremes rather than normals, show the number of adult males and females that have been found on single heads from several parts of the world: Colombo, 257:96, 447:116, 11:30, 28:7, 0:7; Lagos, 14:3, 3:17; Kakamega, 5:1, 0:5, 15:5, 0:7, 7:16, 116:198, 5:24.

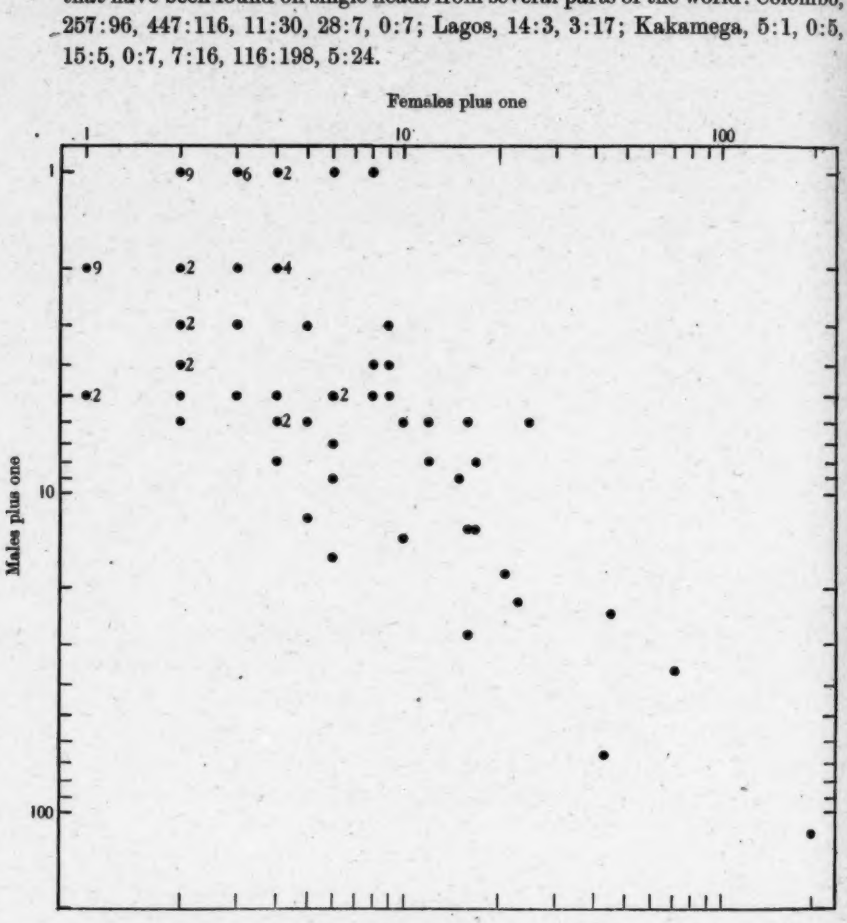


Fig. 1. Showing the number of male and female lice on separate heads from Kakamega, Kenya. The scale is doubly logarithmic for the sake of compactness: it has been necessary to add one to the number of males and females on each head, for there are a considerable number of zeros (e.g. heads with 2 males, 0 females), and zero cannot be shown on this scale.

The same disparity between the sexes in large numbers of heads is also shown in Fig. 1, which gives the number of male and female lice in all the heads from Kakamega in which adult lice occurred (the total number of heads is seventy-eight, not the ninety shown in Table 1, because twelve infested heads contained only young lice). A similar distribution (Fig. 2) shows the numbers

of males and females in 125 infested heads from Colombo. Figs. 1 and 2 show that, particularly when the total number of lice is low, many populations contain only adults of one sex. If one takes the ninety populations from Kakamega, there are thirty-nine in which the total number of lice (including larvae) was ten or less: in these both sexes were present in six (15 %) only, one sex in twenty-two (56 %) and larvae only in eleven (28 %). As a contrast, in the fifty-one heads which contained more than ten lice, both sexes were present in forty-three (84 %) and one sex in eight (16 %).

Table 1. *Showing the total number of populations of head-lice available for study, and the number of them in which there were* 1–10, 11–100 *or over* 100 *lice*

Place	Total infested heads	Heads with 1–10	Heads with 11–100	Heads with 101 and over	Percentage distribution 1–10	Percentage distribution 11–100	Percentage distribution 101 and over
Lagos, Nigeria	21	7	9	5	—	—	—
Sokoto, Nigeria	42	31	9	2	—	—	—
Nairobi, Kenya	37	24	12	1	—	—	—
Kakamega, Kenya	90	39	42	9	43·3	46·7	10·0
Colombo, Ceylon*	125	81	35	9	64·8	28·0	7·2
Cannanore, South-west India	543	356	173	14	65·6	31·9	2·6
Total	858	538	280	40	62·7	32·6	4·7

* Adult lice only (see Buxton, 1938*b*).

In a group of heads, for instance all those from one place, the correlation coefficient (r) is the most convenient way of expressing the degree to which the numbers of males and females are related. In calculating this coefficient one must exclude those heads which contained only larvae (without males or females). The values of n are therefore less than those given in Table 2. The following coefficients have been calculated:

Place	n	r	S.E.
Kakamega	78	0·93	0·11
Cannanore (Hindus)	461	0·80	0·05
Colombo	125	0·83	0·07

Table 2. *Giving the numbers of adult lice and proportion of males in all infested heads from certain places*

Place	No. of infested heads	Total lice: Adults	Total lice: Males	Males as % adults	Diff./S.E.
Lagos	21	516	293	56·8	3·1
Sokoto	42	96	37	38·5	2·2
Nairobi	37	72	30	41·7	1·4
Kakamega	90	1231	528	42·9	5·0
Colombo	125	4180	2346	56·1*	7·9
Cannanore	543	2333	1082	46·4	3·5

* But see Table 4.

It can be seen (Fig. 1) that the correlation is approximately linear in the figures for Kakamega, and we have no reason to think that it is not linear for Cannanore. As to Colombo, it is known that the proportion of males increases

with increasing density of population (below), so that the correlation is not linear, and one would use the coefficient with some hesitation. It need hardly be said that all these coefficients are "significant" (P is much below 0·01 in each case). My personal feeling is that they are surprisingly high, having regard to the erratic ratios observed in some heads.

For purposes of comparison one needs some expression of the proportion of males to females, which may be recorded in a number of different ways. The percentage distribution, i.e. the number of males and females per hundred adults, seems best, because it is the easiest for the ordinary person to grasp: it is sufficient to quote one percentage (the male), the other being obtainable by subtraction.

Though very unequal numbers of males and females may occur in a family, or in the lice on a single head, one might perhaps expect the numbers to approach equality in a group of heads from one place, but this is not so. If one adds together all the figures from each separate locality one obtains the facts given in Table 2: two things are evident, either sex may predominate, and the divergence from equality (50 % of each sex) is often large. The "significance" of this divergence may be tested by taking the difference of the actual percentages from 50, and the standard error of this difference. It is found that in the small sample from Nairobi the difference is not certainly significant: but in the other samples the difference is two or more times its S.E., so that one concludes that it is not due to a sampling error.

One may enquire whether the proportion of the sexes in a family, or in a wild population of *Pediculus*, is entirely determined by the sex chromosomes; or whether some environmental factor produces a mortality which is differential in respect of sex, or even causes a reversal of sex early in the individual's life. (For information relating to insects in general, see Wigglesworth, 1939, p. 404, and references there quoted: also Holdaway, 1932; Holdaway & Smith, 1933.) There are several environmental factors which might perhaps be effective in *Pediculus*.

Type and quantity of hair. One would suppose that the type of a man's hair (length, straightness, etc.) would be an important factor in the life of the head-louse. Probably, therefore, there is a great difference between life on an African scalp (with 5–10 g. of crinkled curly hair) or on a scalp in Ceylon or South India (with 10–30 or even 50 g. of nearly straight hair). But it does not seem that this difference affects the sex ratio: we find that among Africans the percentage of male lice was 56·78 at Lagos, 42·89 at Kakamega, 38·54 at Sokoto: among Asiatics, it was 56·12 at Colombo (but see below) and 46·38 at Cannanore (Table 2).

It seems probable that the length of a man's hair is an important factor in the life of the head-louse. We cannot measure the length, particularly in hair which has been shaved and sent in by post, but measurements of weight of the

crop of hair are available, and it has already been shown (Buxton, 1940*a*) that this is an important ecological factor. The facts from Kakamega, and from Cannanore (Hindus only), have been tabulated to show percentages of male lice in groups of men with different weights of hair. The figures (Table 3) do not indicate any relation between the proportion of males and the hair weight. Similar figures have been worked out for all the other localities: they support this conclusion.

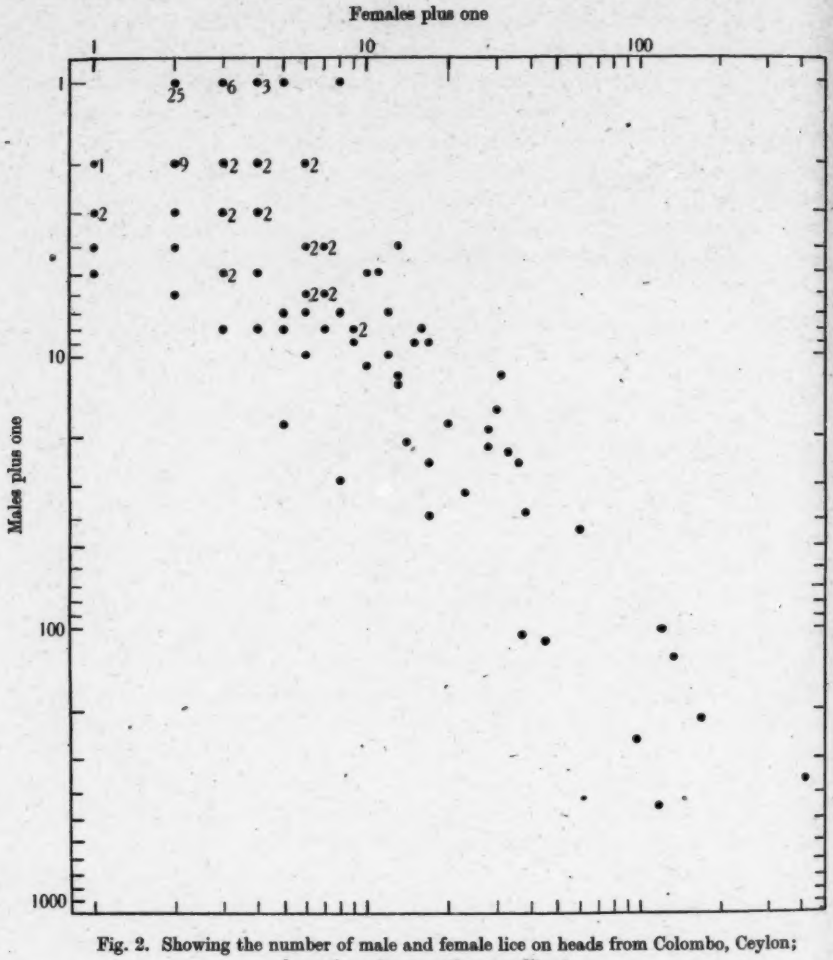
Table 3. *Showing the numbers of adult lice and the proportion of males in infested heads from Cannanore and Kakamega, the heads being distributed according to weight of hair*

N = no. of infested heads, ♂♀ = total adults, % = percentage of ♂♂ in total adults.

Cannanore (Hindus)				Kakamega			
Material	N	♂♀	%	Material	N	♂♀	%
Hair: Up to 9·9 g.	56	111	40·5	Hair: Up to 5·0 g.	33	179	37·4
10–19·9 g.	153	377	43·5	5·1–10 g.	37	460	46·1
20–29·9 g.	118	480	52·1	Over 10 g.	20	592	42·1
30–49·9 g.	108	638	46·4	All weights	90	1231	42·89
Over 50 g.	26	340	48·8				
All weights	461	1946	47·3				

Density of louse population. The number of lice per head tends to be positively correlated with the weight of the host's hair, which has just been shown not to have any regular relation to the insect's sex ratio. It therefore seems probable that the density of the louse population would have no influence on the sex ratio. The facts for Kakamega and Lagos have been worked out, and show no relation between the number of females per head (used as a measure of density) and the percentage of males. The figures hardly justify publication, and similar data from other places have not been tabulated.

The material from men in jail at Colombo, Ceylon, stands by itself because the numbers of lice were unusually high on certain individuals. It will be remembered that 125 heads containing adult lice were examined, and that among them nine contained more than 100 adults, the larvae being uncounted for a reason already given (Buxton, 1938*b*). The proportion of males and females in the 125 is shown in Fig. 2. In Table 4 the figures are tabulated, to show the percentage of males at different densities of population. As to the low proportion of males (30·30 %) in the least dense infestations, I have no explanation to offer, and have not observed the same phenomenon in material from other places. In heads containing from three to twenty-five adult lice the proportion of males is between 45 and 46 %, and we may perhaps regard this figure as normal for the area. When the adult lice are from 26 to 100 per head (and this would be regarded as a heavy infestation in most places) the proportion of males rises, and it rises still more in the nine heads in which the total number of adult lice exceeds 100. The rise in the proportion of males is remarkable, and unquestionably significant.


Females plus one
1
10
100
1
10
100
1000
Males plus one
25
6
3
1
9
2
2
2

It seems probable that this increase in the proportion of males, which is only observed when the density of lice is remarkably high, is explained by certain experiments which have been recently published (Buxton, 1940*b*, Table 2): it was shown that if one kept one young female in a box with six or more males, her life was materially shortened and her daily production of eggs greatly reduced: in a series of experiments the mean life of the female was 8·75 days, the normal being 30·56, the life of the males not being reduced. Clearly then the effect is not due simply to crowding, but to the effect of many males on one female: presumably her death is due to repeated pairing, or to the males' violent attempts to pair. One is probably justified in thinking that something similar occurs in nature when the density of the population has passed a certain point: the figures from Colombo (Table 4) seem to indicate that a differential mortality of the females begins when the number of adults per head is between 25 and 100, and that it is greatly increased when the total passes 100. In effect this gives the population an internal mechanism which prevents it from increasing beyond a certain point; the mechanism is that when the chance of the sexes meeting is very high, the males begin to have an unfavourable effect, therein resembling a predator which is more destructive when the density of prey is highest.

Certain biological factors. As already reported (Buxton, 1940*b*), experiments have been performed in order to discover whether partial starvation, or crowding in early larval life, affects the proportion of the sexes. The experiments were not conclusive, but give no grounds for thinking that any such result occurred. It is difficult to suppose that in nature either starvation or crowding could have any such effect.

In certain other insects, the production of males and females is determined by parthenogenesis, or delayed fertilization, or the sex ratio of the offspring changes towards the end of the mother's life. None of these causes are operative in *Pediculus*.

Climatic factors. In experiments and in nature, lice are maintained on the surface of the body, that is to say under equable conditions of temperature and humidity. But in spite of this, widely divergent sex ratios may be observed; in experiments, one may even have all male and all female families at the same season. It seems to follow that temperature and humidity cannot be effective in altering the proportion of males and females.

Conclusion. From the fact that, under uniform conditions of breeding, one may obtain unisexual or mixed families it seems evident that the sex ratio is determined by the chromosomes alone. It seems therefore to lie with the cytologists to provide us with an explanation of what occurs. The early work of Doncaster & Cannon (1920) and Cannon (1922) will serve as an introduction to the subject. No evidence has been found that any environmental factor has any effect upon the sex ratio (save in the exceptional case where a female encounters a male extremely frequently).

Proportion of larvae and adults

In considering the relation between number of larvae and adults it seems sufficient to limit the enquiry to larvae and females. The gross figures are set out in Table 5.

Table 5. *Showing the material available for study, and the numbers and proportions of females and larvae*

Place	Total infested heads	Lice		Larvae per female	S.E.
		Females	Larvae		
Lagos	21	223	2062	9·25	0·62
Sokoto	42	59	493	8·36	1·32
Nairobi	37	42	459	10·93	1·24
Kakamega	90	703	4409	6·27	0·48
Cannanore	543	1248	6774	5·43	0·41
Total	733	2275	14197	6·24	0·08

In general, one may say that the facts about larvae and females resemble those already studied about males and females. Individual heads depart greatly from the mean, as one sees in Fig. 3, which gives the number of larvae and females in eighty-five heads from Kakamega. In this group the mean number of larvae per female is 6·27, but in several heads the ratio is under three or over ten. One may show this in a different way by grouping all heads which contain a particular number (0, 1, etc.) of females. The sort of result one obtains is shown in Table 6, which gives the data for heads from Cannanore. The scatter in each group is so great that the standard deviation generally exceeds the mean. In considering such facts as these, it would be wrong to think of the lice on a head as a family. If one finds a female and some larvae they may be parent and children, or they may be unrelated, or the female may be the elder sister (newly emerged) of the larvae. This probably helps to explain the great diversity which is found between heads.

Table 6. *Showing the numbers of larvae per head in all heads containing no females, one (two, etc.) females, from Cannanore*

No. of females per head	No. of heads	Larvae per head			S.D.
		Max.	Min.	Mean	
Nil	211	45	0	4·03	6·58
One	153	37	0	4·48	7·18
Two	53	75	0	12·79	14·81
Three	34	75	0	12·59	15·67
Four	15	73	6	21·93	18·09
Five	19	87	0	25·11	21·88
Six	8	65	14	33·87	54·87

None the less, though there are many aberrant members in the group, there is a clear tendency for the numbers of larvae and females to be related (Fig. 3). For Kakamega the correlation coefficient is $0·87 \pm 0·11$: for Cannanore it is $0·72 \pm 0·04$. One feels some surprise that the coefficients are so high.

Larvae plus one

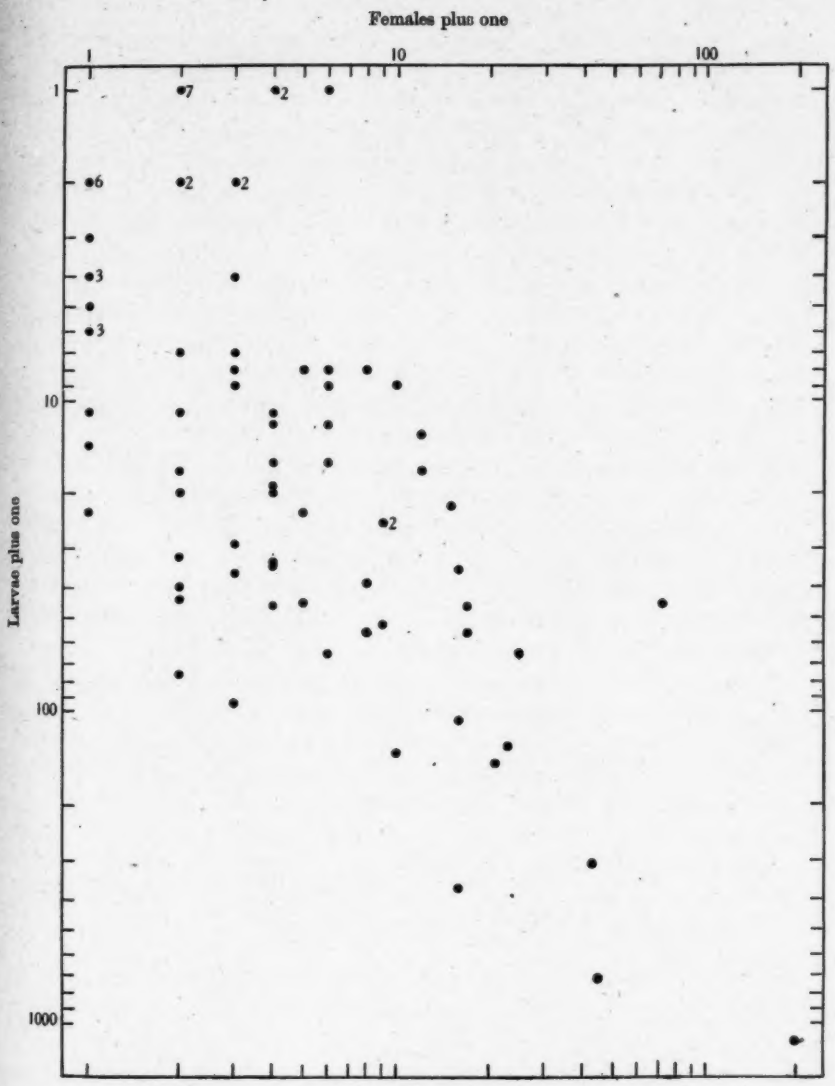


Fig. 3. Showing the number of females and larvae on separate heads from Kakamega, Kenya; for scale and conventions see Fig. 1.

If one considers the mean number of larvae per female, one finds large differences between different localities. At Lagos, Sokoto and Nairobi, the mean lies between 8 and 11; but at Kakamega it is 6·3, and at Cannanore 5·4 (Table 5). Between any two of the first three places the difference cannot be regarded as significant; all other differences, including that between Kakamega and Cannanore, exceed twice their S.E. and are significant.

One is inclined to suppose that some environmental factor may account for these great differences in the number of larvae per female, in different samples. Our general knowledge of the biology of *Pediculus* suggests several factors which might be effective.

Type and quantity of hair. We have already seen that the difference between Asiatic and African hair does not seem to be associated with any constant difference in sex ratio. Similarly, it appears not to affect the number of larvae per female: for instance, though the number is high in three African collections (Lagos, Sokoto, Nairobi) it is low at Kakamega (Table 5).

Weight of hair, already known to be a variable important to the louse, might have its effect on the number of larvae per female. For this, the best available figures are those from Cannanore, for the range of weight of hair is so great. The figures (Table 7) at first sight seem to show that as weight rises there is a fall in the number of larvae per female, but the correlation coefficient (−0·69) might occur by chance about one time in ten, and cannot be regarded as significant. One notices that in the first weight group (up to 9·9 g.) the number of larvae per female is very high.

Table 7. *Showing the relation between weight of hair, and the number of larvae per female, in material from Cannanore (Hindus only)*

Hair weight g.	No. of infested heads	No. of lice		Larvae per female
		Female	Larvae	
Up to 9·9	56	66	569	8·62
10–14·9	75	77	453	5·88
15–19·9	78	136	646	4·75
20–29·9	118	228	1399	6·14
30–39·9	63	231	1167	5·07
40–49·9	45	111	487	4·39
50·0 and over	26	174	785	4·51
Totals	461	1023	5506	5·38

It is hardly likely that samples of hair from Africa would show a relation between weight of hair and larvae per female, for the range of weight of hair is not great. The figures for Kakamega are:

Hair weight g.	Heads	Females	Larvae per female
Under 5·0	33	112	9·64
5·1–10·0	37	248	4·50
10·1 and over	20	343	6·35
All weights	90	703	6·27

Figures for Sokoto, Nairobi and Lagos show a similar absence of relation. In the above figure for Kakamega, the number of larvae per female is high in

the first weight group, as it is at Cannanore (Table 7); but it is not high at the other African localities.

Density of louse population. The data from Cannanore have been divided into groups, containing 0, 1, 2, etc., females: there is no evidence that the number of larvae per female rises or falls with the number of females. One should, however, remember that at Cannanore the density is never very high: only fourteen heads were found in which the total number of lice exceeded 100. Colombo is the only place in which I have found considerable numbers of larger populations of lice; unfortunately, the figures for larvae at Colombo must be disregarded as already explained (Buxton, 1938*b*).

It is also possible that the number of larvae per female might be less in those heads in which there is an excess of males. Some time has been given to considering this, the Cannanore material being sorted according to whether the number of males was above, equal to, or less than the number of females. No relation was discovered between masculinity and the number of larvae per female.

Climatic factors. It will be remembered that the temperature and humidity in the hair are much more stable than they are in the general atmosphere. But, on the other hand, weather and season have such great effects on man, and on his occupations, that they might also, though indirectly, affect his parasite. Indeed, it has already been shown that the rate of infestation in certain places (Sokoto, Kakamega, Agra and perhaps elsewhere) is to some extent influenced by season (Buxton, 1938*b*), though we do not yet know what elements in climate are effective.

One might therefore find that the season or climate would cause alterations in the ratio of larvae to females (either by an effect on births, or on larval deaths). But a general consideration of the gross figures in Table 5 does not give much ground for thinking that this is so: the number of larvae per female is not significantly different in Lagos which is damp and equatorial and Sokoto which has a monsoon climate, with a short very wet season and a long rainless period. Moreover, one sees that though the climates of Nairobi and Kakamega (both in Kenya) are not unlike, the ratios of larvae per female are quite different (10·93 and 6·27). Prima facie, it seems that climate is not likely to be a major factor.

One may go rather further, taking a relatively homogeneous group such as the Hindus at Cannanore, and searching for a seasonal change in the number of larvae per female. The most striking seasonal change in the climate of the Malabar coast is in the rainfall, which is very heavy from May to October, and nil for the other six months. The Hindus show the following figures:

Months	Females	Larvae	Larvae/♀
May to Oct.	412	2202	5·34
Nov. to April	610	3305	5·42

Similar figures have been worked out for separate hair-weight groups: even in this more homogeneous material no evidence is found that the number of larvae per female is consistently higher or lower at one season.

It will be remembered that in Sokoto the climate is sharply divided into wet and dry seasons, and that there is evidence that people are more often infested in the dry season (Buxton, 1938*b*). The total amount of material is not great, and (in any one age group) fails to show any difference in the number of larvae per female. From the figures from Kakamega one draws a rather similar conclusion. If one excludes males up to ten years old and all females, the following figures are obtained, the months June to October being the colder and wetter:

Months	Infested heads	Females	Larvae	Larvae/♀
June–Oct.	33	150	749	4·99
Nov.–May	33	492	3012	6·12

The difference in the number of larvae per female in the two seasons is not quite twice its standard error, and one cannot regard it as convincing.

Reviewing the data as a whole, one cannot say that a seasonal difference in the number of larvae per female is proved to exist at any of the places studied. But it seems probable that if an abundance of material were collected at some place in which the seasons are sharply contrasted, such a difference might be discovered. That would be of great interest, for it would point to factors which may influence the rate of increase of populations of lice in nature.

Proportion of the three larval instars

In *Pediculus* there are always three larval instars, and it is not difficult to distinguish them. The lice recovered from hair from Cannanore (but not from other places) have been preserved in spirit, and my colleague, Dr Haddow, undertook to examine a part of them, so as to determine what proportion of larvae belonged to each instar. The work is laborious, for every specimen must be put under the microscope, and a good many must also be measured. It was easy to distinguish first instars, by the short abdomen and the few setae in regular longitudinal rows on the dorsum of the abdomen. The second and third instars are less easy to separate. It was found most convenient to measure the third tibia; it has been shown that, at least in body-lice, this measurement gives a clear difference between instars. In the present material no doubtful cases were encountered; the absolute measurements were rather less than those published by myself, probably because the head-louse tends to be smaller than the body-louse in most respects. Occasionally, if the legs were bent or damaged, second and third instars were distinguished by points in the chaetotaxy (Buxton, 1938*a*).

After he had examined all specimens from the first fifty-one infested heads, Dr Haddow considered the results and desisted, for it seemed doubtful if the

labour was justified. These fifty-one heads were unselected: they were the first infested heads met with in the inquiry and were collected from May to August 1937. In them there were 142 males, 154 females, and 502 larvae, a total of 798. The larvae yielded the following data:

	Numbers	%
1st instar	218	43·4
2nd instar	189	37·7
3rd instar	91	18·1
Indeterminate	4	0·8
	502	100·0

The reduction from first stage to second is 13·3 %, from second to third 51·8 %. As we know that the length of life of the three instars is approximately equal, it is clear that the death-rate is very far from regular; indeed, it is four times as high in the third instar as in either of the other two. Moreover, the deaths occur during the course of the third instar: if they occurred at the beginning or the end of it (for instance at the final moult), that would not produce the figures obtained. As to the cause of these deaths, we are ignorant. It will be remembered that under experimental conditions, if body-lice are reared in boxes on myself, there is a high death-rate early in the first instar, and that this is believed to be due to artificial conditions (Buxton, 1940*b*). From this it is evident that the course of mortality among larval head-lice in nature and body-lice in boxes, is entirely different.

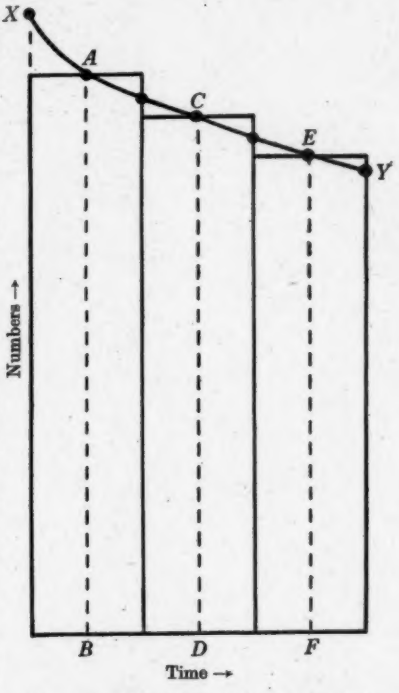


Fig. 4. Hypothetical case in which the three instars (shown as rectangles) are reduced by mortality at a steady rate.

Perhaps I may set down a line of argument, which would lead to new and valuable conclusions, though it is not applicable to these figures. Let us suppose that we are dealing with some insect in which the number of instars is known and invariable, and that the length of time passed in each is also known: furthermore, on analysing a population, evidence has been found that mortality is at a steady rate through larval life (which it is not in *Pediculus*). We may represent the facts by a diagram (Fig. 4) in which each instar is shown as a rectangle, of which the base is proportional to the length of life of the instar: in the case

chosen for illustration there are three instars, and their duration is supposed to be equal. If there are a large number of insects in each instar, then one may say that the average one is half-way through its life in that instar: the lines *AB*, *CD*, *EF* will therefore represent the numbers in each instar. But as the mortality is at a steady rate (by definition) these numbers fall on a geometrical progression. One may therefore extrapolate and find the points *X* and *Y* on the same geometrical progression. These points give one the number of first instars which succeed in hatching from the egg, and the number of last instars which reach the final moult. There are certain circumstances, depending on the nature of each case, under which those figures might point further to conclusions of value.

The line of argument appears to be of considerable potential value: it may be adapted according to the particular insect under study.

Discussion

The subject of insect populations is one to which many workers, in pure and applied science, will turn in the future: there are a number of possible ways of approaching it. A population is essentially dynamic, in the sense that it is always increasing or decreasing, and exhibiting change in the proportion of larvae and adults in it. But if one takes a large number of populations, as we have in this paper, one may think of them as static; for instance, in the village as a whole the lice will not be increasing, for the gain on one head will be offset by the loss on another. It seems therefore legitimate to study events at a particular moment, even though one knows nothing of what led up to them.

The author has had the good fortune to deal with an insect of which the biology is extremely simple and well known. Each race of *Pediculus humanus* lives its whole life in a single environment; in this environment, temperature and also humidity tend to be stable. There is one food only, human blood, for adult and larva, and the supply of this is for all practical purposes unlimited, so that there is no competition for food. A simple method has been evolved for collecting the hair from the people who are to be studied, and for separating the lice from it; complete crops of nearly 3000 people from several parts of Africa and Asia have been studied. In the present group of papers I have already reported on the human side of the question; for instance, the relation of infestation to the human being's age, sex, race, etc., and to seasonal factors (Buxton, 1936, 1938*b*, 1940*a*). In the present paper we turn to the entomological side of the problem, and discuss all the actual infestations, which number 858.

To sum the matter up, we have an unusually favourable field for study; the insect's life history is simple and well known; there is abundant material, and it has been studied and tabulated in a variety of ways. Indeed, the writer has had a very unusual opportunity of discussing the relation of a parasite to

a vertebrate host. What comes of it? Do any points of general interest come out of this solid effort?

This is not the place to summarize the first three papers, but it is appropriate to call attention to certain general points which have emerged from that work; there is a strong positive correlation between weight of hair (which is the best measure we have of length of hair) and infestation: there is a negative correlation with age, boys tending to be more infested than youths, who are more infested than men. It has been possible to formulate one general rule; if one takes a large group, such as all the heads from one place, and divides them into subgroups (e.g. by age, or weight of hair) then those subgroups in which the proportion infested is highest are also those in which the highest counts of lice are found.

Another general point is that though the biology of *Pediculus* is simpler than that of the great majority of insects, the distribution of lice among men is complex. This is probably due, at least in part, to the complexity of human affairs. We observe for instance that in one part of Africa, at Sokoto, infestations are commoner in the hot season, and in another part, at Kakamega, in the cool, wet season; the explanation of the anomaly may well lie in the agricultural or social customs of the people. In a similar way, one cannot doubt that if a man with the necessary ethnological knowledge were to study the distribution of head-lice among people in certain parts of Asia or Africa, he would reveal the extent to which it is influenced by such things as hair dressing and hair cutting, and by all the customs which bring certain members of society into contact with others. All those complexities wait to be discovered; they must be studied on the spot, not in London.

It seemed at one time that one might be able to deduce the approximate mortality among the larvae from the number of larvae per female. I felt that data relating to the body-louse (Buxton, 1940*b*) might be used, in the absence of figures about the head-louse. As the biology of the insect is simple, particularly in respect of temperature and food supply, one may suppose that the daily production of eggs is uniform; and as a large population (on many heads) is stable, the proportion of larvae to adults does not change. I then took particular values for the female's length of life and daily production of eggs (Buxton, 1940*b*), and made certain assumptions about the mortality of eggs and larvae. If we first consider a simple but unnatural case, and assume that there is no mortality in the early stages, also that the female lays nine eggs daily, the duration of the egg stage and also of larval life being 9 days, then there might be as many as eighty-one larvae per female alive, excluding grandchildren. It will be observed that this figure of eighty-one is not affected by the length of the female's life, except when the female's life is under 9 days. But it is evident that this simple case has no relation to reality. One has to suppose that a certain proportion of eggs and of larvae die; but we know

nothing about the mortality in either stage, and we may not suppose that the death-rate is the same in the egg and larval stages. We are therefore left with three major unknown factors, which are independent of one another so far as we know, the mortality of the egg and that of the larva, and the mean reproductive life of the female. There are many different combinations of these three variables, though not an infinite number, which would produce a particular figure for the number of larvae per female. No further progress seems possible at the moment, though the matter can be taken up again when we know more about the quantitative biology of lice, particularly of the head-louse. Data on the mortality of eggs in nature or on the length of life of marked females would be of great value. There is, however, one general conclusion which may even now be drawn. We know that in a large group of heads the mean number of larvae per female is five or ten or some such figure (Table 5). This must imply a very large mortality in the eggs or the larvae; there must therefore be some cause of death which acts differentially on early stages. Further than that we cannot now go.

This series of papers may be concluded on a note of depression and humility. We have studied a very simple and well-known insect, and have looked at it in a new way. A large amount of material has been collected and analysed, and very little that is positive has been found. All through the four papers the writer has continued to report failure to demonstrate any relationship between infestation and some natural event which one would have supposed to be a relevant factor.

Summary

1. In three previous papers (1936, 1938*b*, 1940*a*) the author has discussed the distribution of head-lice among their human hosts, his material being nearly 3000 complete crops of hair. The present paper deals with the strictly entomological side of the inquiry, that is to say, with the study of the populations of head-lice themselves. The total amount of material is the lice from 858 infestations from six places; from each of four places there were less than 100 infestations.

2. In about two-thirds of the infestations there were ten lice or less, the proportion of low infestations varying considerably from place to place (Table I). Infestations over 100 never formed more than 10 % of all the infestations in a place.

3. In a single head the proportion of the sexes is often far from equal; indeed, in light infestations it is common to find that all the adults are of one sex. Taking all the heads from one place, the total number of males and females differs significantly from equality, an excess of males occurring in one place, of females in another (Table 2). In all heads from one place the coefficient of correlation between the number of males and females is high, about 0·8–0·9. As the density of the louse population does not generally affect the

sex ratio, the correlation is approximately linear. But when the density is unusually high, as it is in some heads from Colombo, the proportion of males rises progressively. This is the only case known, in spite of much searching, in which sex ratio of the louse is affected by an environmental factor.

4. In the matter of the number of larvae per female, there are great individual differences between heads, though the coefficient of correlation, worked on all the heads from one place is as high as 0·7 or 0·9. Taking all the heads from one place, the mean number of larvae per female ranges between 5·4 and 10·9; many of the differences between places are significant. I have failed to find any explanation of these differences, and they do not seem to be affected by any environmental factor. The fact that the larvae are always more numerous than the females, indicates that there is a high mortality during the course of larval life; the author has failed to make a more precise estimate of the proportion which die.

5. A small part of the material was specially examined, and every larva referred to its instar. In this sample of 502 larvae it was found that the death-rate was higher in the third instar than in the other two, a state of affairs the reverse of what occurs in body-lice reared in boxes.

Acknowledgements have already been made to those who collected the material, and helped by treating the raw hair and sorting the large amount of numerical fact. Let me here thank Dr A. B. Hill for advice on statistical problems, and Dr A. J. Haddow for long hours spent on the raw data of the present paper.

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THE EFFECT OF TEMPERATURE UPON THE HATCHING OF THE EGGS OF *PEDICULUS HUMANUS CORPORIS* DE GEER (ANOPLURA)

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(With 1 Figure in the Text)

Summaries of the effects of temperature upon the time required for the hatching of the eggs of *Pediculus humanus corporis* given by Nuttall (1917) and by Buxton (1939) show that when kept at constant temperatures[1] the lower limit for hatching is between 22 and 25° and 16 days is given as the incubation period at 25°. The upper limit is stated to be between 38 and 40° (5 days at 37°).

The present work was begun to discover the period of exposure necessary to kill all eggs at a number of different temperatures.

In batches of eggs of *Pediculus* reared artificially the percentage hatching varies even when they are taken consistently from the same person. Eggs used in these experiments were therefore taken from several cultures reared in pillboxes on the legs of two, three or four persons. The age of the eggs was known to be less than 24 hr.

After the eggs had been counted, the pieces of black tape on which they were laid were placed (with the eggs still attached) in small Petri dishes (*not* in tubes). A piece of black material had previously been secured to the bottom of each dish to afford foothold for the newly emerged larvae. The Petri dishes were kept in closed desiccators over mixtures of sulphuric acid and water thus providing a constant relative humidity in each vessel. Temperatures were controlled electrically in the incubators containing the desiccators, recorded by thermographs and checked by mercury thermometers.

Eggs incubated at constant temperatures

By keeping newly deposited eggs at constant temperatures it was found that they would hatch between 24 and 37°. They would not hatch at 23° or lower, or at 38° or higher. The figures for these experiments are given in Table 1 and are plotted on the graph (Fig. 1). It is seen that at temperatures near the upper and lower limits the percentage of eggs successfully hatched is reduced; also that at low temperatures the incubation period is lengthened. Temperatures which could be considered as favourable are between 29 and 32°. At any one temperature, humidity did not affect the duration of the incubation period though extremely low or extremely high humidities reduced the percentages of eggs hatched (Table 2).

[1] The temperatures in this paper are given in degrees Centigrade.

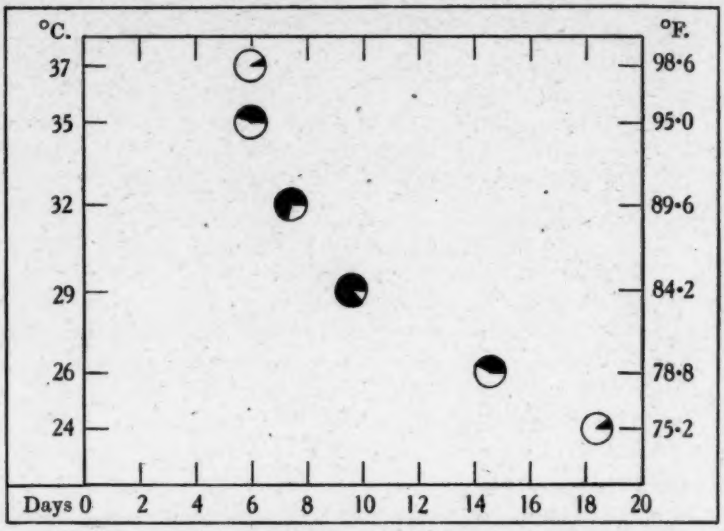

Fig. 1. Mean incubation period of eggs of *Pediculus* at constant temperatures. Black segments represent proportion hatched.

Table 1. *Temperatures at which* Pediculus *eggs hatched*

°C.	No. eggs used	No. eggs hatched	% eggs hatched	Duration of incubation period in days	Mean incubation period in days
37	269	24	9	6– 7	6
35	379	170	45	5– 7	6
32	471	342	73	7– 9	7·5
29	438	386	88	9–11	9·5
26	381	168	44	13–19	14·5
24	120	14	11	17–21	18

Table 2. *Hatching of eggs of* Pediculus *at different temperatures and humidities*

°C.	% relative humidity	No. of eggs used	% eggs hatched	Duration of incubation period in days
37	10	89	0	—
	50	90	22	6– 7
	95	90	4	6
35	10	56	25	6– 7
	50	72	25	6– 7
	75	106	72	5– 7
	90	89	38	5– 7
	95	56	50	5– 7
32	45	92	75	7– 9
	65	261	79	7– 9
	85	118	57	7– 9
29	30	146	86	9–11
	60	148	97	9–11
	90	144	80	9–11
26	25	71	41	14–19
	50	79	46	14–17
	75	80	62	13–15
	90	79	30	14–17
	95	72	39	14–18
24	90	120	11	17–21

EFFECT OF "UNFAVOURABLE" TEMPERATURES UPON HATCHING

Eggs were exposed to different "unfavourable" temperatures for definite periods and then transferred to a "favourable" temperature, 30, 31 or 32°, for hatching. A relative humidity of 65 % was used throughout the experiments.

At 39° experiments were done to discover how soon eggs were killed at this temperature. More than 100 eggs were used in each experiment. They were kept for periods of 1–7 days and then removed to 32°. Only eleven out of 105 eggs hatched; these had been kept for 1 day at 39°; six of them hatched on the sixth day after removal to 32° and the other five hatched on the seventh. The remaining eggs were kept for another 11 days but no more hatched. Thus 2 days or more at 39° killed all the eggs.

Eggs were kept at 24° for different periods and then transferred to 32°. As the period at 24° was lengthened the incubation period at 32° shortened. For example, eggs which spent 7 days at 24° commenced to hatch on the sixth day at 32°, but those which spent 14 days at 24° began hatching after only 2 days at 32°. Eggs kept continuously at 24° commenced to hatch on the seventeenth day and hatching continued until the twenty-first day. This was the lowest temperature at which eggs successfully hatched.

Eggs were exposed to 23° for periods ranging from 3 to 40 days. No eggs hatched at this temperature, though a number of eggs developed eye-spots. After the time spent at 23°, eggs were removed to 32°. The only hatching that occurred after the transfer was among eggs which had previously spent 11 days or less at the lower temperature. In each case hatching commenced on the sixth day at 32°. No eggs hatched at 32° among batches which had spent a previous period of 14 days or longer at 23° (Table 3).

Table 3. *Eggs of* Pediculus (*under* 24 *hr. old at commencement*) *exposed to* 23° *and then to* 32° *until hatched*

No. of eggs	Days at 23°	Days at 32°	Days to hatch at 32° and no. hatched	% eggs hatched at 32°
42	3	8	6 (10) 7 (7)	40
86	6	11	6 (13) 7 (3)	18
50	7	9	6 (15)	30
50	9	12	6 (5)	10
30	10	9	6 (14) 7 (4)	60
33	11	11	6 (4)	1
70	14	20	—	—
90	15	11	—	—
50	19	14	—	—
115	20	13	—	—
72	40	0	—	—

By exposing eggs to 22 and 20° it was found that eye-spots developed in some of the eggs though no hatching occurred. Some of the eggs hatched after removal to 32° before the eleventh day at 22° and the tenth day at 20°, but

they did not hatch if they were removed after 14 days at these temperatures. Short preliminary exposures to 22 and to 20° resulted in the subsequent incubation period at 32° being extended beyond the normal and long exposures reduced it (Table 4).

Table 4. *Eggs of* Pediculus (*under 24 hr. old at commencement*) *exposed to 22° for different periods and then to 32° until hatched*

No. of eggs	Days at 22°	Days at 32°	Days to hatch at 32° and no. hatched	% eggs hatched at 32°
102	4	14	9 (34) 10 (26) 11 (1)	60
93	5	13	8 (12) 9 (7) 10 (1)	22
107	6	13	8 (26) 9 (15)	38
105	7	12	7 (1) 8 (11) 9 (8)	19
45	8	10	7 (3)	7
115	9	11	6 (10)	9
100	10	11	6 (6)	6
66	14	9	—	—
100	15	13	—	—
103	16	12	—	—
100	17	11	—	—
143	22	16	—	—
104	41	7	—	—

Eggs were kept at 19 and 18° and moved to 32°; at 15 and moved to 30°; at 10 and moved to 31°; and at 8 and moved to 32°. No eggs hatched while they were at 19° or below. After the transfer to higher temperatures, no eggs hatched among batches which had spent 7 days or more at 19° or below. Among eggs which had spent 6 days or less at these low temperatures hatching occurred after the transfer to the higher ones. They commenced to hatch at each of the favourable temperatures in the minimum normal incubation periods as follows: at 32° in 7 days, at 31° in 8 days, and at 30° in 9 days. The percentages which hatched were lowest among those batches which had spent the longest periods at the preliminary low temperatures. To illustrate this the figures for 8 and 32° are given in Table 5.

Table 5. *Eggs of* Pediculus (*under 24 hr. old at commencement*) *exposed to 8° and then transferred to 32° until hatched*

No. of eggs	Days at 8°	Days at 32°	Days to hatch at 32° and no. hatched	% eggs hatched at 32°
120	1	13	7 (85) 8 (18)	86
103	2	12	7 (36) 8 (11)	46
80	3	11	7 (4) 8 (10) 9 (1)	19
113	4	10	7 (24) 8 (9)	27
103	5	11	7 (1) 8 (1)	2
44	6	13	7 (2)	4
104	7	12	—	—
104	8	11	—	—

Eggs nearly ready to hatch

Batches of eggs were incubated for 6 days at 32° and then transferred to 23°. They were kept at this temperature for 1, 3, 5 and 7 days and then restored to 32° unless they had already hatched. In all the batches hatching com-

menced on the first day at 23° and continued for two more days. Therefore, eggs in an advanced stage of development will hatch at 23° though, as we have seen, newly deposited eggs kept at this temperature do not.

Eggs incubated at 32° for 6 days were exposed to 19° for 6, 7 and 8 days and then returned to 32°. Some eggs hatched at 19° on the fourth day and others on the seventh and eighth days. A larger number of eggs hatched after they were put back to 32°. A temperature of 19° is therefore not low enough to prevent the more advanced embryos completing their development.

Similar experiments were carried out with eggs incubated at 32° for 6 days and then at 18°. Some eggs hatched at 18° every day from the second to the ninth. Also, a considerable proportion hatched after being restored to 32°, except when the period at 18° was 8 days or more.

Eggs incubated for 7 days at 31° were stored at 15°. No eggs hatched at 15° and none hatched after being replaced at 31° if the period at 15° had been more than 9 days (Table 6).

Table 6. *Eggs of* Pediculus *incubated at* 31° *for* 7 *days, exposed to* 15° *for different periods and then transferred to* 31° *until hatched*

No. of eggs	Days at 31°	Days at 15°	Days at 31°	Days to hatch at 31° and no. hatched	% hatched at 31°
29	7	1	6	2 (20) 3 (6)	90
40	7	3	8	2 (22) 3 (7)	73
50	7	5	9	1 (8) 2 (20) 3 (4)	64
27	7	6	12	1 (7) 2 (8) 3 (3)	66
28	7	7	12	1 (8) 2 (8) 3 (2)	64
53	7	8	12	1 (5) 2 (30)	66
30	7	9	30	—	—
53	7	10	29	—	—

In a rather similar way, eggs were incubated at 32° and then exposed to 8° just before they were expected to hatch; they did not hatch, but they were not killed unless the period at 8° was over 9 days.

Table 7. *Minimum times of exposure to constant temperatures which ensure that eggs of* Pediculus *are killed*

°C.	Newly deposited eggs days	Older eggs
8	7	9 days
10	7	9 days
15	7	9 days
18	8	Some eggs will hatch
19	9	
20	10	
22	12	
23	14	

Partially developed eggs

A few experiments were done with eggs incubated at 30° for periods of 2–5 days and then exposed to 15° for 1–10 days. No eggs hatched while they were at 15°. When they were replaced at 30° larvae hatched in those batches in which the period at 15° had been from 1 to 7 days. Longer periods at 15° were fatal.

Conclusion

It has been shown that eggs of lice are killed by short exposure to high temperatures (39° and over) but medical officers and others interested in the control of lice will gather from these experiments that the eggs may also be killed by exposing them to low temperatures (28° and below). The period of exposure necessary varies of course with the temperature and with the stage of development of the eggs. The minimum periods required are shown in Table 7. It will be seen that in dealing with a mixed collection of eggs the temperatures should not be above 15° and the exposure should be not less than nine days.

Summary

The hatching of the eggs of *Pediculus humanus corporis* De Geer is influenced by temperature.

High temperatures accelerate and low temperatures delay development.

The lowest constant temperature at which eggs will hatch is 24° and the highest 37°.

At 24° eggs begin to hatch on the seventeenth day and continue hatching until the twenty-first. At 37° eggs hatch on the sixth and seventh days. The temperature at which eggs hatch in the shortest time is 35° and the time 5 days. At these extremes many eggs are killed so that the percentages of successful hatches are very low. Eggs are killed by 2 days' exposure to 39°.

Temperatures at which the maximum number of eggs hatch lie between 29 and 32°. In this range of "favourable" temperatures, up to 97 % of successful hatches may be recorded. The incubation period is from 7 to 11 days. This is a convenient range of temperatures for laboratory purposes and gives largest numbers in a reasonably short time.

Newly deposited eggs will not hatch if kept for 14 days at 23° or for shorter periods at lower temperatures, until at 8° exposure for 7 days is sufficient to ensure that all eggs are dead.

If partially developed eggs are exposed to temperatures of 15° or lower, development ceases. If they are restored to a favourable temperature within 7 days, development is resumed and some of the eggs will hatch.

Older eggs which have almost reached hatching point at a "favourable" temperature hatch if transferred to temperatures as low as 18°. They do not hatch at 15° or lower if kept at such temperatures for at least 9 days.

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